The Journal of HEREDITY

ONLY ONE SET OF CHROMOSOMES
(SEE PAGE 107)

Soviet Genetics at the Botanic Congress

New Linkages in the Tomato

Vigor in Pine Hybrids

VOLUME 42 MARCH-APRIL, 1951 NUMBER 2

The American Genetic Association

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The JOURNAL OF HEREDITY is published bi-monthly by the AMERICAN GENETIC ASSOCIATION at 32nd Street and Elm Avenue, Baltimore 11, Md., and 1507 M St., N. W., Washington 5, D. C. Address all communications regarding editorial matters to 1507 M St., N. W., Washington, D. C. Communications regarding the business management of THE JOURNAL OF HEREDITY may be addressed to the publication office, 32nd Street and Elm Avenue, Baltimore, Md., or to 1507 M St., N. W., Washington 5, D. C. Entered as second-class matter February 24, 1923, at the postoffice at Baltimore, Maryland. Acceptance for mailing at the special rate of postage provided for in section 1103, Act of October 3, 1917, authorized December 29, 1918.

Contents copyrighted 1951 by the American Genetic Association. Unauthorized reproduction of material from THE JOURNAL not permitted. The title "Journal of Heredity" is registered as a trade-mark in the U. S. Patent Office.

$5.00 a Year. $1.00 a Copy. Prices of back numbers on application.

The

Journal of Heredity

Vol. XLII MARCH-APRIL, 1951 No. 2

CONTENTS

Marxist Genetics at the Stockholm Botanical Congress
By Åke Gustafsson 55

New Evidence on the Genetics of the Palomino Horse
By W. E. Castle and F. L. King 61

A Species Cross in Cucurbita
By Thomas W. Whitaker 65

The "Vestigial Tail" Mouse
By W. E. Heston 71

Interspecies Hybrids in Pines
By F. I. Righter and J. W. Duffield 75

A Goat With Heteronymous Horns
By H. Epstein 81

Cytogenetic Studies on Buckwheat
By M. Rosalind Morris 85

Polyembrony in Maize and Lily
By D. T. Morgan, Jr. and R. D. Rappleye 91

A Genetic Bud Mutation in the Pear
By C. F. Reimer 93

Effects of Water Source on Toxicity of Mercurial Poisons
By Eileen W. E. Macfarlane, Sister Alma Marie Messing and Sister H. Hilaire Ryan 95

New Linkage Groups in the Tomato
By L. Butler 100

A Method for Analyzing Multiple Allelic Inheritance
By D. C. Rife 105

Monoploidy in Nicotiana
By August F. Kehr 107

Notes and Reviews

A Moratorium on Science? 59

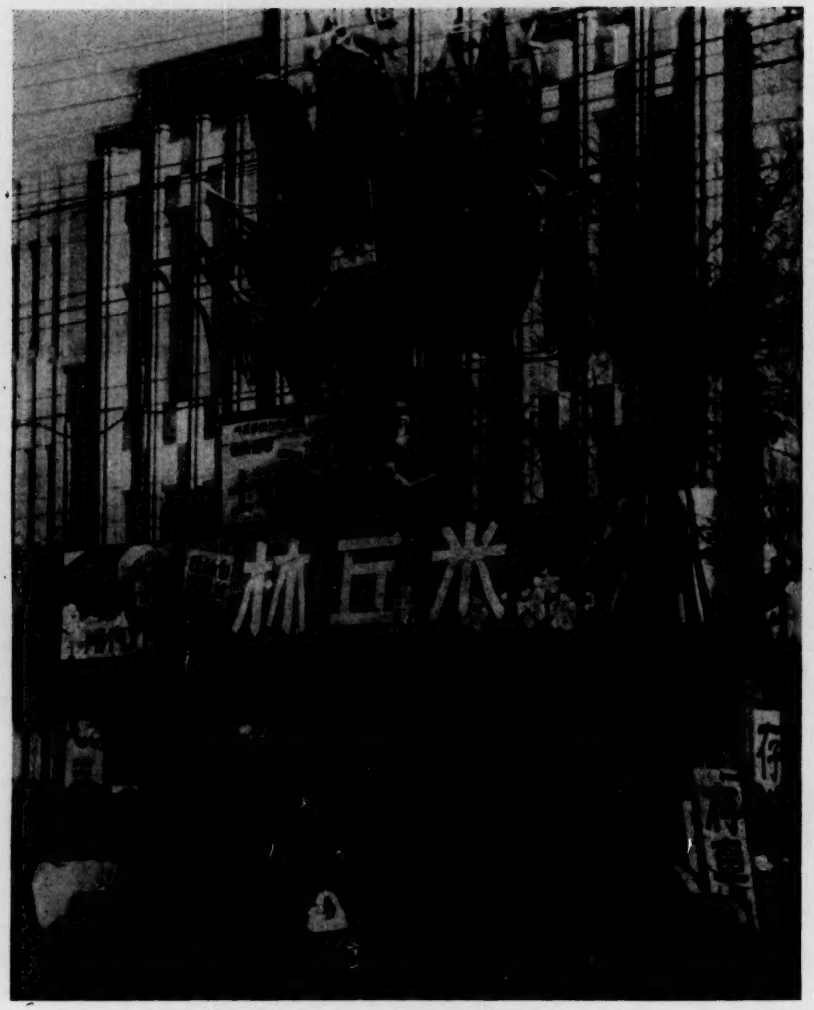
Michigan State Fellowships Announced 64

Communist Biology in Peking and Moscow 69

Science in Hungary 70

The Hemophilia Foundation 74

Symposium on Genes and Mutations 94



MICHURIN COMES TO PEKING

Figure 1

This official "Sovphoto" records the opening in Peking of a double feature Communist propaganda film-fest. The large poster over the foyer announces the showing of "Michurin"—no doubt the same film shown in New York in 1948 under the title "Love in Bloom" (See JOURNAL OF HEREDITY for July 1949). The name Michurin appears in Russian characters under the portrait of the patron of Marxist genetics at the left end of the panel. The large Chinese characters in the center of the panel are a phonetic transliteration in ideographs of the word "Michurin." The small panel to the left identifies Michurin as "the great originator of new plant forms." Also featured in Chinese: the film is in Technicolor, and the sound-track in Chinese. The Soviet caption accompanying the photographs calls attention to the "throngs at the entrance of a movie house in Peking." That Michurin rates second billing only to Stalin in this display emphasizes the important place that Marxist genetics holds in communist propaganda plans (See page 69).

MARXIST GENETICS AT THE STOCKHOLM BOTANICAL CONGRESS

ÅKE GUSTAFSSON

VISITORS FROM MOSCOW

Figure 2

Members of the Soviet delegation to the Botanical Congress in Stockholm in the summer of 1950 visiting the experimental plots of the Swedish Seed Association at Svalöf. Dr. A. Akerman (extreme right) is showing some of his wheat experiments to three Soviet botanists: Glutschenko (face in deep shadow), Soukatsjev and Henkel (facing Akerman). In the background are the Swedish geneticists Drs. Muntsing, Levin, and Gustafsson. On his return to Russia, Glutschenko wrote of this meeting that the delegates showed "great interest" in Lysenko's "discoveries" and singled out several Western scientists for attack as "reactionaries."

GREAT artists and scientists are often said to be misunderstood by their contemporaries and only long afterwards obtain the recognition they earned. It would be ridiculous to deny that this might happen today also. In the Soviet Union, (but only there), Michurin is recognized as the founder of modern biology and Lysenko is his prophet. Are we western scientists wrong when we deny their theses? Are the Russian biologists who applaud them, freely or on the order of the Communist Party, ignorant frauds, deliberate frauds or merely ignorant?

There was a good opportunity to compare Western genetics with militant Lysenkoism, as the latter was presented at the 1950 Botanical Congress of Stockholm by the Russian delegates, Professors Soukatchev, Henkel, Gludtschenko, Baranov, Suchov, Turbin, and Stoletov. We wanted to analyze their data quietly and composedly, to display our own material, to admit them right if they convinced us, but to adhere to our views if we still regarded them as true. The Russian delegates were

treated in exactly the same manner as the other members of the congress. They were the guests of a Swedish congress and of Swedish institutions, and they were our colleagues in scientific discussions.

Right here let me stress the point that the Russian delegates, and the accompanying members of the legation too, behaved entirely as gentlemen, if this Anglo-Saxon word may be used, the corresponding Russian expression being unknown to me. The female interpreter was very agreeable, indeed charming. Nothing singular could be detected in her manner, except that she shuddered strongly and paled, when a dynamite charge was quite peacefully exploded outside the windows of the Swedish Seed Association at Svalöf, where the Russians gathered for a lecture of introduction one day after the congress. Her reaction should not be misunderstood, however. We cannot forget that the Soviet Union was for four years involved in a bitter fight for life or death with the then enemy number one of the democratic world.

Some of the delegates are known as good, even high-ranking botanists. This is especially true of their official leader, the seventy year old professor of the Forest Research Institute of the Academy of Sciences, V. N. Soukatchev. In significant papers dealing with the competitive and productive abilities of biotypes in *Taraxacum* (dandelion) he has published results in full agreement with Mendelian ideas. Professor P. A. Henkel, who spoke a fluent German, is well-known as a plant physiologist.* The noisy debater of the delegation was powerful Professor I. E. Gludtschenko, a defender of Lysenko's ideas, who by a singular stroke of fate happened to be the first visitor to the newly inaugurated John Innes Horticultural Institute at Bayfordbury, England, the director of which, Dr. C. D. Darlington, is a bitter opponent of Lysenkoism. The other four botanists were second plane figures. Professor Baranov, however, reported some interesting findings in his congress lecture.

Although the Russian delegates as individuals acted entirely as gentlemen, they rather severely attacked, on the other hand, those branches of biology which take chromosomes and genes into consideration. They openly proclaimed that Mendelism is metaphysical, that real achievements can be obtained only according to the principles of dialectical materialism, and that Western biology has arrived at a deadlock owing to its "idealism." Even Professor Soukatchev apostrophed, indeed idealized Lysenkoism in his lecture on plant ecology. This implies, as we regard the matter, nothing but an empty gabbling that has no real bearing on our experiments and their reliability. Personally I got the impression that the professors who declared themselves geneticists (Gludtschenko, Suchov, Turbin, Stoletov) believed in Michurin's and Lysenko's theses, but that the others just acted in agreement with the orders of the Communist Party. In fact, I am almost certain of this interpretation.

Graft Hybrids and Spore Tetrads

A central theme of all discussions consisted of Lysenko's assertion that heredity can be changed by means of grafting. Here Gludtschenko repeated the words of the master but did not add anything new about the experiments, so successful in the Soviet Union but not confirmed outside it. He did not mention or try to analyse Winkler's findings of so-called burdans, which imply possible fusion products of vegetative nuclei from stock and scion (1934, 1936), still less their rareness compared with regular chimaeras or uninfluenced partners of the graft. At the long discussion of a late Monday night in July he displayed his lack of knowledge in fundamental Mendelism. In fact, he himself more or less indirectly admitted so at the end of the session. He was insistently, although in a quite friendly way, pushed against the wall by the repeated questioning of a Portuguese scientist from distant Mozambique, Professor Quintanilha. As Quintanilha pointed out, there is a simple arrangement, illustrating Mendelian segregation in lower organisms. It deals with the number of different cells from a single spore tetrad (the so-called tetrad analysis). In individuals heterozygous for one gene difference we obtain the spore distribution of 2 : 2 (or 4 : 4 in the Ascomycetes), not 2.1 : 1.9 or 1.7 : 2.3, but exactly 2 : 2 in any spore tetrad derived from an individual spore mother cell. We conclude that Mendelian segregation is in principle a definite, not just a statistical process. In fact, it is possible to separate the two categories of spores under the microscope, cultivate them separately and so find out their exact position in the tetrad (or octad in the Ascomycetes). There is in my opinion no question of the fact that this fundamental result was unknown to the Russian professor. After a week of debates, at Stockholm, Lund and Svalöf, he and his colleagues finally admitted in public that chromosomes do have a *certain* influence on the mechanism of heredity but still proclaimed, "opposing the Mendelians," that other mechanisms are at work too. However, this is not denied by any modern geneticist. In fact, some prominent representatives of Mendelian thought (Correns, von Wettstein, Michaelis, Sonneborn) have performed clear experiments to prove that it is so. Thus the Lysenkoists, as new but more successful Don Quixotes, are attacking windmills.

The Soviet biologists use two types of argument. First, they declare that Darwin's theses have become more or less forgotten outside the Soviet Union, where the fire is kept burning owing to the efforts of Lysenko. Rather comically, however, Lysenko does not include

*He knew all terms and definitions of modern genetics but declared himself a physiologist.

GLUTSCHENKO AND WINGE
Figure 3

Soviet delegate Glutschenko confers with conference chairman Oyvind Winge of Copenhagen before the meeting at which Glutschenko addressed the conference. Nina Matveyeva, official translator for the Soviet delegation, stands between them. An ardent Lysenkoist, Delegate Glutschenko appeared to be ignorant of many of the established principles of genetics. He and his colleagues admitted, however, after the Congress was over, that chromosomes do have some influence on heredity!

under his definition of Darwinism what is really the essential theme, the selection theory, the struggle for existence, but continuously adheres to Darwin's view on the gradual changes of heredity by environmental conditions, not presented in the first edition of his "Origin of Species." The Russians use arguments from the later editions, where Darwin had altered his phrasing and added to or subtracted from his original theses. Consequently they attack from a wrong angle, from a point of view which ought to have repelled rather than attracted them, namely Darwin's compromises with the conservative or even reactionary elements of church and science.

Secondly, the Russian biologists—in agreement with comrade Lysenko himself — over and over again fell back upon the supposed shortcomings of Mendelism to improve on the material status of a people. Here they argue against better knowledge, or at least against facts. For instance, so far as Swedish plant-breeding is concerned, which I know fairly well, its recent methods are entirely built up on theoretical achievements whether in valuable species like *Pisum sativum,* in ornamental plants like *Antirrhinum,* in useless organisms like *Drosophila,* or in harmful species like mice. By these methods Sweden has finally succeeded in becoming self-supporting with regard to cereal production. Our present wheat, oats and barley varieties have been produced, not in spite of, but due to the intentional application of Mendel's laws. All sugar now obtained in my country originates from seed material that is raised annually by purposeful intercrossing of 20 different strains, selected for their high combining ability. And to add an example from the United States, nobody but an ignoramus dares to deny that hybrid corn, the use of which has resulted in gains of hundreds of millions of dollars, owes its origin to more than twenty years of theoretical research.

Swedish plant-breeders reason that up to 40 or 50 percent of the gain in annual yield since the end of the last century depends on improved strains obtained as a result of continu-

ous breeding work. The remaining half of the gain is due to plant husbandry, to careful drainage, increased amounts of fertilizers, better weed and insect control. But plant breeding and plant husbandry do not oppose, rather they support and condition one another. The improved soil conditions require new strains able to endure high nitrogen dressings and to allow a fully mechanized type of agriculture. It is false to separate them and then evaluate them individually. I especially wish to stress this fact. We may safely conclude that the planned type of plant breeding, not haphazard in character, is necessary for the progress of any country. Plant breeding should rest on *all* our present knowledge, not on the fifty year old ideas of Lysenkoism.

From the numerous discussions in which I took part, at Experimentalfaltet, Stockholm and Svalöf, I venture the conclusion, entirely in my capacity as a free scientist, influenced by no political prejudices, not even by my ideals of personal freedom, that Lysenkoism did not get itself into a better light as a result of the Russian visit. It remains as loose and unscientific in character as it has always been. Note for instance the nonsensical postulates, repeated over and over again, that hexaploid *vulgare* wheat can easily arise from tetraploid *durum* wheat or that a hardy winter wheat will suddenly arise from a spring variety, according to the time of sowing. Eventually Lysenkoism will lead to a catastrophe for Soviet agriculture, if it is not swept away in time. Personally I think with sad horror of the numerous citizens who will suffer from starvation on account of triumphant Lysenkoism. In this connection I must express my deep admiration for early Soviet biology, which in such a profound way contributed to the development of science. Many of its representatives are now dead, some are able to work but cannot possibly influence public opinion, others live in foreign countries.

Despite this negative outcome the visit confirmed what we knew before, i.e., that the Russian leaders regard science and scientists with a high esteem and put enormous annual sums at their disposal. In this respect it teaches us a good deal. Often and willingly many leading Swedish politicians—I am purposely sticking to my own country—expatiate on a theme of planned national development. However, they certainly plan the development of science very poorly, if at all. With a wider type of research, greater financial support and more attention to new ideas from the young generation, Sweden ought to be able to increase public welfare considerably and to gain in economic strength. Present research all over the world is characterized by a remarkable synthesis of allied subjects and a clear apprehension of the fertility of adjoining sciences. The political leaders go on, however, without bothering too much about these new aspects. I shall choose one example. Even now, fifty years after the rediscovery of Mendel's laws and ninety years after Darwin's "Origin of Species" there is no planned teaching or research in genetics at the oldest and largest of the Swedish universities. Genetics, and the theory of evolution, have brought botany, zoology, chemistry, geology and more recently physics close together. By excluding genetics from the University of Uppsala, old ideas, in this case unfruitful dogmatism of the post-Linnean type, prevent the full development of Swedish biology. Others than Lysenko and his followers represent past century thought. I understand that this is also valid for countries other than Sweden. The crude division into teaching *or* research, practical accomplishments *contra* theoretical work, which I have found to characterize some colleges and universities in the United States, is as I see it extremely short-sighted. To me the good teacher must be a good scientist. Otherwise he cannot gather around him a circle of promising young men. Furthermore, practical work and theoretical analysis do not exclude each other, in fact they cannot be separated. They fit together like improved straw-stiffness and high manuring in recent Mendelian agriculture.

Gludtschenko's Report

In an article in the *"Tägliche Rundschau"* (Berlin) for Sept. 15, 1950, Gludtschenko has informed us about his views on the Stockholm Botanical Congress. He specially entered into the shortcomings of Blakeslee and Darlington. "The theoretical significance of his—i.e. Blakeslee's—work is very limited, and there is no need to lose a word on its practical value." About Darlington he writes: "Not a single question was directed to the speaker [after the lecture]. But in the corridors it was stated how boring, uninteresting and reactionary were his theses."

There is no need to dwell too long on these comments. They should be read in the original. Under the heading "Michurin's biology founds a school" (Die Mitschurinsche Biologie macht Schule) Gludtschenko indicates, however, that a splitting has occurred among the "formal" geneticists abroad. The Swedish botanists Heribert Nilsson, Müntzing and Levan exemplify, according to him, such a splitting of thought. Either our Russian colleague does not know the actual situation, misunderstands what happened or deliberately distorts the facts. Anyhow, he is entirely wrong. Heribert Nilsson may oppose *Drosophila* work and the current emphasis on induced mutations but he adheres to strict Mendelism. His position is that genetics of 1940/50 had better return to the time of original Mendelism, when genes were still firm, unchangeable units. He has never stated his views about Lysenkoism in print but he detests all sorts of Lamarckism, including the Russian brand. Gludtschenko writes about Müntzing and Levan: "The Swedes were very interested of this experiment"—the conversion of winter rye into summer rye—. . . [and] "promised to repeat it

and had to admit that it could not be explained according to Morganism." If Gludtschenko believes that the scientists mentioned were converted to Michurinist theories by vague statements, he is greatly mistaken. He then adds: "Many western biologists begin to understand that the theories of Weismann and Morgan have been disproved. They acknowledge the power and activity of the Michurin biology. So the unusual interest of these scholars for the lectures of the Soviet delegates can be explained." His conclusion is, I dare state, nothing but propaganda. And with regard to the character of Swedish genetics, it is simply a lie.

Be that as it may. The Soviet Russian visit to the Stockholm Congress, so auspicious from a general point of view, unfortunately confirmed the fact that the Russian biology of today is not what it once was. It proved that the fame of Trofim Lysenko rests on a chimaera, if this expression be pardoned me. As an agronomist he possibly promoted the increased mechanization of agriculture. As a scientist he is uncritical and biased. Finally, as a biologist, he has destroyed what was so successfully built up by Soviet scientists who now exist no more. Ultimately, if not swept away, his ideas will ruin Soviet agriculture.

✦

A MORATORIUM ON SCIENCE?

"WHATEVER its shortcomings, science alone is not to blame for the trials of civilization. We are neither wise enough nor good enough to live the way we would like to live. All the factors and forces of civilization have not enabled us to reach the goal. Perhaps 'There has been more progress in intelligence than in kindness.' But would ignorance make us kinder; and would kindness make us wiser? Would it be wise to become more ignorant in the hope of thereby becoming kinder and wiser? Should there be a moratorium on science until the spirit can overtake the intellect? . . .

"The need of science is greater than ever, because the world is figuratively smaller and actually much more crowded than ever before. Human problems, therefore, are more complex, and more intelligence and ethics required to solve them. . . .

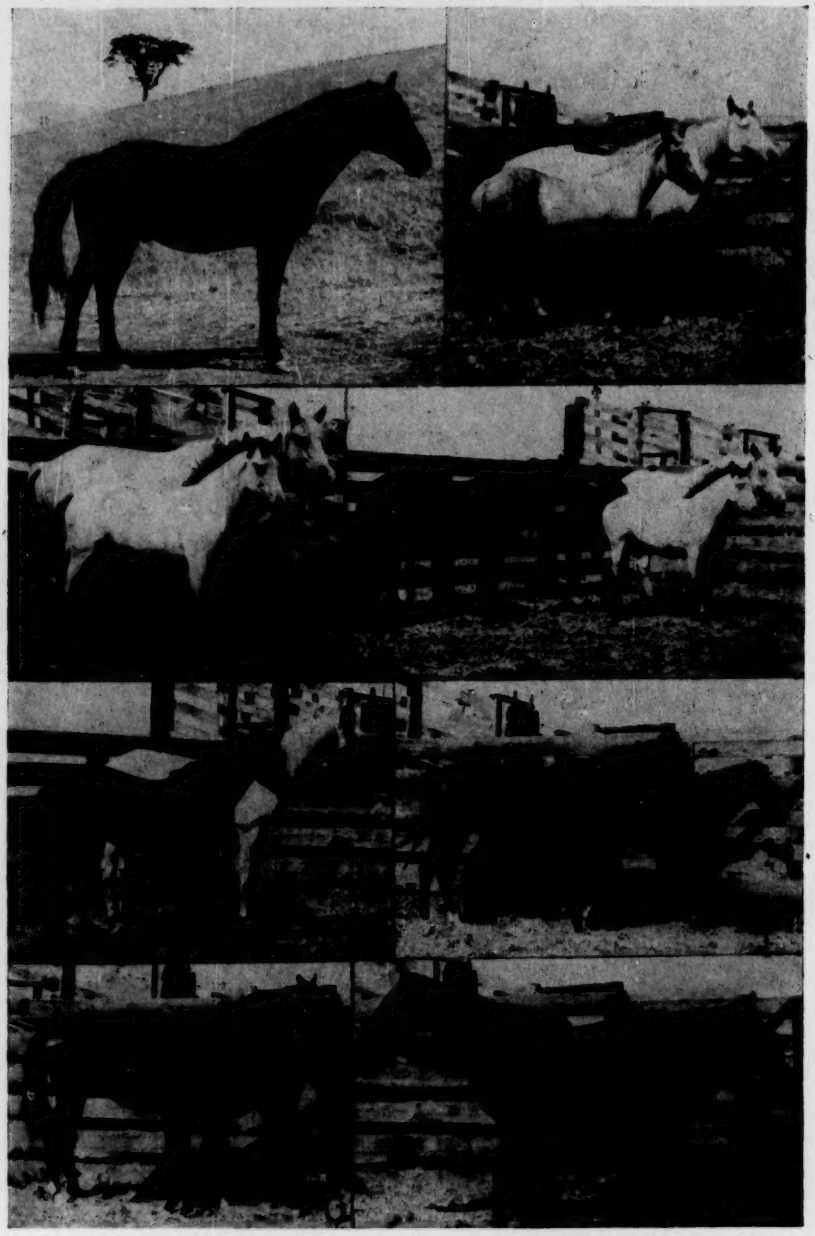
"What alternatives have countries with too little land? They can reduce their standard of living, increase agricultural efficiency, industrialize and trade, reduce population, live on charity, starve, or swarm and kill or be killed. Some countries still can choose one of the first three alternatives; some, like Japan, are restricted to the last three. It does not solve the problem of overpopulation to say that it never should have come into existence. It does exist, and it must be faced. The problem is basically biological, although its basic nature is often obscured. There is a tendency for biological entities to swarm when they press too heavily on means of subsistence. This is true of potato bugs and grasshoppers, of wolves and human beings. The struggle for existence is not restricted to lower organisms; nor are the uglier aspects of the survival of the strongest restricted to them.

"What can science contribute to the solution of problems arising from maldistribution of people and resources? It can insist on objective analysis of the problem; it can help solve the biologic and technologic problems involved, within the limits imposed by nationalism. But it cannot, under present conditions, solve the political problems involved. For nationalism often is epistatic to science, to ethics, and even to religion. Science has solved many problems of man in relation to his physical environment, but it has not succeeded in emancipating man from his baser self, from man's cruelty to man. Can science contribute to better human relations? . . .

"Can insistence on a scientific attitude gradually help substitute facts for fancies; principles for prejudices; education for propaganda; intellectual integrity for mental cleverness; statesmanship for partisan politics; broad humanitarianism for tribalism; the Golden Rule for the law of the jungle? Can science help human beings act the part? Can it contribute both to wisdom and to ethical conduct? This should be the ultimate goal of science. . . .

"A moratorium is needed, but it is a moratorium on the conflict between science and the humanities. For science, religion, music, art, history, literature, have values in the degree to which they make men happier, wiser, and better. The value of each varies with individual men. All are valuable insofar as they illuminate the intellect, refine the spirit, and stimulate useful and ethical conduct. To promote truth, wisdom, and justice is not the prerogative of any one guild. The factors and forces in the evolution of the human intellect and spirit are varied and complex; and it is unscientific and unethical to deny to each its fair share of credit for its contributions.

"Humanity needs both the sciences and the humanities; both are humanizing to the extent to which they humanize. There is need for more understanding and tolerance between scientists and humanists; properly motivated, all are humanists and their joint contributions can accelerate man's evolution toward intellectual enlightenment and spiritual refinement.—E. C. STAKMAN. *Science*, February 19, 1951. pp. 140-142.



PALOMINO AND RELATED PHENOTYPES

Figure 4

A—is the heterozygous stallion Black Traveler (*ddBbaa*). *B* is the albino mare "Chubby" (*DDbbA*—) and her Palomino colt. Her Palomino colt is heterozygous for the *D* locus. *C* is the Palomino mare "Sally" (*DdbbAa*) and her buckskin colt (*DdBbA*—). *D* shows the same mare with two other colts by Black Traveler. One is black (*ddBbaa*) and the other is Buckskin (*DdBbAa*). *E* shows the Palomino mare "Quinta" (*DdbbAa*) and her dilute black colt (probably *DdBbaa*). *F* shows the chestnut mare "Katy Fleming" (*ddbbA*—) and her chestnut colt. *G* and *H* show chestnut mares "Barbara" and "Dessie" (*ddbbA*—). The former has a black colt and the latter a bay colt.

NEW EVIDENCE ON THE GENETICS OF THE PALOMINO HORSE

W. E. CASTLE AND F. L. KING*

DURING the past several years the breeding operations of one of the author's (F.L.K.) have accumulated data regarding color inheritance which makes possible a reappraisal of the problem of Palomino color. More than a hundred colts have been classified to give the data presented in this analysis.†

Basic Genes in Color Inheritance

Mammals in a wild state, unaffected by domestication, have in common three genes (inheritance units) involved in the production of their coat color. These have been designated *A*, *B*, and *C*.[2]

C (color) is the designation of a dominant gene which is indispensible to the production of melanin pigment in the hair and skin. If *C* mutates to a state of inactivity (*c*) albinism results, expressed by the genetic formula *cc*, showing that albinism is recessive to color in inheritance.

B (black) designates a dominant gene which, in cooperation with *C*, produces black pigment. All wild mammals, so far as our present knowledge goes, possess these two genes and so develop a black pigmented coat. But the coat is rarely uniform black. As a rule the black pigment is distributed in a pattern of regionally different concentrations of black, intermingled with regions in which a red-yellow pigment is shown. Such a wild coat pattern is determined by a dominant gene which may be designated *A*. It is so designated because it was first identified in rodents, where the wild coat pattern is strikingly shown in the South American agouti. Gene *A* in rodents stands for the agouti type of coat. Use of *A* may appropriately be extended to the wild-pattern gene in mammals generally. In horses it will designate the gene for the ancestral coat pattern seen in the wild Prejvalski horse and in the domesticated *bay* horse.

The genes *A*, *B*, and *C* are all dominant in inheritance. Their recessive alleles, *a*, *b*, and *c*, when homozygous, result in mutant novelties as follows:

aa results in uniform black, complete absence of the wild coat pattern. *bb* results in pigment changed from black to brown, a less completely oxidized melanin pigment. *cc*, as already stated, results in albinism, complete absence of pigment.

Basic Color Genes of Horses

All horses have a coat more or less heavily pigmented. This is sufficient evidence that they possess a color gene, *C*. No recessive mutation of this gene is found among horses, a mutation which would result in true albinism, *cc*. But reduction in intensity of the pigmentation does occur in some horses through a dominant mutation resulting in a *dilute* general pigmentation. This we may assign to the action of a gene *D*, dilution.

A heterozygous state of the dilution gene, *Dd*, results in moderate reduction of the intensity of all pigmentation, whether black, brown or red-yellow in character, as seen for example in Palomino and buckskin horses. A homozygous state, *DD*, of the dilution gene results in a much greater reduction of the intensity of the pigmentation, as seen in the very pale pigmented individuals produced in Palomino breeding. These have a very pale cream colored coat, almost white, with pink skin and blue eyes. They are popularly called "albinos," though they are not true albinos, which result only from recessive mutation of the color gene. But for convenience we shall employ the popular term "albino" for a homozygous dilute (*DD*) horse otherwise of the genotype of a Palomino.

That dilution is not a result of mutation in the color gene, *C*, is shown by the following fact. When heterozygous dilute horses, *Dd*, are bred together, three genotypes result: *DD*, *Dd*, and *dd* in a 1:2:1 ratio. The genotype *dd* is of full intensity, showing that it possesses the color gene *C*, as do also the *DD* and *Dd* genotypes.

A heterozygous dilute horse, brown pigmented (*Ddbb*), is exemplified in the Palomino. See Figure 4*B-D*.

A heterozygous dilute horse, black pigmented (*DdBb*), is exemplified in the buckskin or dun. See Figure 4*C-D*.

A homozygous dilute horse, brown pigmented (*DDbb*), may be called a "type A albino." See Figure 4*B*.

A homozygous dilute horse, black pigmented (*DDBb*), may be called a "type B albino."[2] See Figure 4*E*.

*University of California and Lafayette, California, respectively.

†This report has been written by W. E. Castle, but the experimental evidence which it contains was produced by F. L. King. A large share of the credit for any increase in knowledge which may result belongs to Mr. King.

The doubly dilute (*DD*) or "albino" type of horse is not considered desirable by breeders, but a heterozygous dilute, particularly the brown pigmented (Palomino) variety, is considered highly desirable. What, then, are the essential genetic constituents of a Palomino?

Essentials of the Palomino Genotype

Salisbury and Britton[5] concluded, on the basis of their own studies, as well as on those of several earlier investigators, that the essentials of the Palomino genotype are (1) a heterozygous state of the dilution gene (*Dd*) and (2) a homozygous state of the brown gene (*bb*).

We shall show that a third necessary constituent of the Palomino genotype is gene *A*, for the ancestral wild bay coat pattern. This gene, being dominant, is effective either when heterozygous (*Aa*) or when homozygous (*AA*). Accordingly, as regards the three essential constituent genes, the genotype of a Palomino will be *DdbbAa* (or *AA*).

A Palomino has a cream or "golden" body color, brown pigment being largely eliminated from the body and concentrated in mane, tail and legs by the action of the bay pattern gene, *A*. The predominantly brown pigmentation of mane and tail, being lighter optically than the red-yellow pigmentation of the body, results in mane and tail color being reported as "light" or "white."

The Crypto-Palomino

If a Palomino lacked *A* in its genotype, being thus of genotype *Ddbbaa*, it would not be recognizable as a Palomino because its pigmentation would be uniform diluted brown all over. We might call it a *crypto-Palomino*.

Examples are found in pedigrees kindly supplied by Dr. H. Arthur Zappe, Secretary-Treasurer of the Palomino Horse Breeders of America, to Professor P. W. Gregory of the College of Agriculture at Davis, who loaned them to us for study.

1) A Palomino colt, Melody Beau, PHBA 9590, was produced by parents both of which were registered as chestnut. Accordingly, one of them must have been dilute (*Dd*) in order to transmit dilution to the Palomino colt. Almost certainly it was the mare, Gayley Legs, both of whose parents were recorded as "cream" (*Dd*) and as such would have been capable of transmitting dilution to their offspring. Consequently, it would appear that Gayley Legs lacked only the *A* gene to make her a typical Palomino, and that her genotype was *Ddbbaa, crypto-Palomino*.

The gametic union which resulted in the production of a Palomino colt by Gayley Legs mated with a chestnut stallion must have been egg *Dba* + sperm *dbA* = *DdbbAa*.

Four other cases are found in the pedigrees supplied by Dr. Zappe in which a registered chestnut mated with a bay produced either a typical Palomino or a buckskin, two cases each. These demonstrate with especial clearness the *crypto-Palomino* nature of the parent registered as chestnut, since a bay horse cannot harbor the dilution gene *D*, for if it did, it would be recognized as buckskin. The conclusion is inescapable that in each of these four cases, the parent recorded as chestnut was really dilute chestnut, a *crypto-Palomino*, genotype *Ddbbaa*, as was Gayley Legs.

The four chestnut horses shown to be dilute by their production of a Palomino or a buckskin colt, when mated with a bay, were: (1) the stallion Billy Wood, ASHBA 19635; (2) the mare Rachel Atkins, ASHBA 15867; (3) the stallion Billy the Kid, AQHA 3226; and (4) the stallion Oklahoma King, TWHBA 431617.

The Crypto-Buckskin

Evidence that a mare described as black or "brown" may in reality be a dilute black, a *crypto-buckskin*, is shown in two pedigrees supplied by Dr. Zappe.

The black mare, Minnie A, had a buckskin dam and a chestnut sire. By a chestnut stallion, in whose pedigrees for two generations no dilute individual is recorded, she had a typical Palomino colt. It appears accordingly that she had inherited dilution from her buckskin dam and transmitted it to her Palomino colt. Her genotype would thus appear to have been *DdBbaa*, and the gametic union which produced her Palomino colt to have been, egg *Dba* + sperm *dbA* = *DdbbAa*.

The other demonstrably dilute black mare was Miss Montez, recorded by the Jockey Club as "brown." Mated with the recorded chestnut stallion, Wise Sir, she produced a dun (buckskin) colt, Wise Abe, JC 394337. The genotype of Miss Montez is thus shown to have been *DdBbaa*. The gametic union involved in the production of her buckskin colt, Wise Abe, was egg *DBa* + sperm *dbA* = *DdBbAa*.

A *crypto-buckskin* horse, when recognized as different from ordinary black, is frequently designated "mouse" or, as in the case of Miss Montez, "brown."

Breeding Tests of Genetic Theory Regarding Dilution

What is believed to be a dilute black (*crypto-buckskin*) colt was obtained by Mr. King in his 1950 crop of colts sired by the stallion Black Traveler. The demonstrated genotype of this stallion is *ddBbaa*. By the Palomino mare Quinta (genotype *DdbbAa*) he sired a black colt suspected of being dilute. It is lighter in color than the black colt shown in Figure 4*G*, neither of whose parents were dilute and which, consequently, could not have been dilute. Quinta's colt also has whitish hairs inside its ears, another indication of dilution or scarcity of black pigment. If this interpretation is correct, the gametic union involved in

the production of this colt was, egg *Dba* + sperm *dBa* = *DdBbaa*, a *crypto-buckskin*.

Other matings of Black Traveler with dilute mares were as follows. (1) He was mated with the homozygous dilute type A albino, Chubby, shown with her Palomino colt in Figure 4*B*. Chubby's genotype is *DDbbAa* (or *AA*). The colt was produced by a gametic union, egg *DbA* + sperm *dba* = *DdbbAa* (Palomino). (2) He was mated with the Palomino mare Sally, shown in Figure 4*C* with her buckskin colt, and in Figure 4*D* shown with the same buckskin colt and her black colt produced in 1939, likewise sired by Black Traveler. The gametic unions involved in their production were (1) egg *DbA* + sperm *dBa* = *DdBbAa* (buckskin), and (2) egg *dba* + sperm *dBa* = *ddBbaa* (black).

Types of Mating Productive of Palomino Colts

It is known that Palomino colts may be produced by four different types of mating involving dilution: (1) Palomino × Palomino, theoretically producing 50 percent of Palomino colts, 25 percent of chestnut colts, and 25 percent of type A albinos. (2) Palomino × chestnut, theoretically producing 50 percent each of Palomino and of chestnut colts. (3) Type A albino × chestnut, theoretically producing 100 percent of Palomino colts. (4) Type A albino × Palomino, theoretically producing 50 percent each of Palomino and of albino colts.

The first type of mating is at present essential to qualification of a colt for registration by the Palomino Associations as a genuine Palomino, although it is only 50 percent effective in producing Palomino colts. The same degree of ineffectiveness inheres in matings of type 2 and type 4, which also produce only 50 percent of Palomino colts, and which are not eligible for registration. Yet type 2 matings produce no albinos and so are preferred to type 1 by some breeders.

Type 3 matings theoretically should produce 100 percent of Palomino colts, if all possess gene *A* in their genotype. It is thus twice as effective as either of the other types of mating in producing Palomino colts in quantity, all of which however would be disqualified for registration by the Palomino Associations. Type 4 matings, like types 1 and 2, should result in producing 50 percent of Palomino colts, but the other 50 percent in this case should be type A albinos.

It may be of interest to inquire how nearly these theoretical expectations are realized in practical breeding of Palomino colts.

The most extensive experiments known to us, which include matings of all four types, are those of Dr. R. V. Morledge of Billings, Montana and those of Mr. King. These will now be reported as summarized by the respective investigators.

Type 1 matings, Palomino × Palomino produced colts as follows:

	Chestnut	Palomino	Albino
Reported by Morledge	20	39	17
Reported by King	1	6	0
Total	21	45	17
Expected	21.75	43.50	21.75 ± 2.23

The numbers of chestnut and Palomino colts are close to theoretical expectation, and the departure from expectation (deficiency) on the part of the albino class is not statistically significant.

Type 2 matings, Palomino × chestnut, produced colts as follows:

	Chestnut	Palomino
Reported by Morledge	45	44
Reported by King	15	13
Total	60	57
Expected	58.5	58.5 ± 3.65

The agreement with the theoretical equality of the two expected classes, chestnut and Palomino, is excellent. Albinos are not expected.

Type 3 matings, albino × chestnut, produced colts as follows:

	Palomino
Reported by Morledge	30
Reported by King	25
Total	55
Expected	55

Agreement with theoretical expectation is here perfect.

Matings identical in character with those of type 3 except that they involve mating an albino to a black pigmented instead of to a brown pigmented (chestnut) mate may be summarized as type 3ª matings.

Type 3ª matings, albino × bay or black, produced colts as follows:

	Palomino	Buckskin
Reported by Morledge	6	2
Reported by King	6	3
Total	12	5

Since both Palomino and buckskin colts are *Dd* in genotype and differ only as regards the *B* gene, these 17 cases may be added to the 55 cases reported for type 3 matings, making a total of 72 cases conforming perfectly to the theoretical expectation that a type 3 or 3ª mating will produce only Palomino or buckskin colts (both *Dd*), none being either nondilute (*dd*) or albino (*DD*), as in matings of type 1.

Type 4 matings, albino × Palomino, produced colts as follows:

	Albino	Palomino
Reported by Morledge	6	0
Reported by King	5	3
Total	11	3
Expected	7	7 ± 1.36

The deviation from the expected equality of the two classes is insignificant in the case of King's observations and of doubtful significance in the combined total of 14 colts reported by both observers.

White Mane and Tail

An essential characteristic of a typical Palomino horse is a mane and tail lighter in color than the body in general, and usually described

as white or flaxen. Three possibilities exist as to its genetic nature.

(1) The simplest hypothesis is that it is an incidental effect of the dilution gene *D*, which acts more strongly on brown pigment, (the major component of the pigmentation of mane and tail), than on red-yellow pigment, (the major component of the general body pigmentation). An analogy for such a differential action is seen in pink-eyed yellow mice and rats, which have abundant yellow pigment in the part of the coat which contains yellow in the wild agouti genotype, but very little black or brown pigment in the eye or skin, where black is predominant in the wild agouti genotype. Differential action of the pigment reducing mutation, pink-eye, greater in the case of black-brown pigment than of yellow pigment, is thus shown to occur in mice and rats. If in horses the pigment reducing action of the dilution gene is similarly differential, this would explain the light mane and tail of Palomino horses.

(2) Another possibility is that light mane and tail are due to the action of a gene other than *D*. It is known that light ("flaxen") mane and tail occur in some sorrel (chestnut) horses which do not possess the *D* gene, as well as in some Shetland ponies. Wentworth[6] explained this as due to a recessive gene, which we might call *f*, flaxen, and which accordingly must be homozygous in order to be effective. Salisbury and Britton[5] accepted this interpretation with qualification, and Castle[2] adopted it tentatively. It may be that the hypothetical gene *f* is responsible for light mane and tail both in sorrel horses and in Palominos. If so, Palomino horses which lack *ff* should not have light mane and tail. If such Palominos exist, they have not as yet been identified.

(3) A third possibility is that the extremely light (white) mane and tail of Palomino horses is due to the combined action of *D* and *ff*. If this is so, Palominos which are *Ddff* in genotype should be lighter than those which are *Dd* but lack *ff*.

Further investigation is needed to determine which of these hypotheses is correct.

Summary

Essential genetic components of the Palomino gentoype are (1) a heterozygous state of the dilution gene (*Dd*), (2) homozygous state of the gene for brown pigmentation (*bb*), and (3) now clearly demonstrated, the bay pattern gene *A*, either homozygous or heterozygous.

Whether white mane and tail are produced as an incidental consequence of *D*, or of a special gene for flaxen mane, *f*, or by the combined action of both in the presence of *bbA*, is uncertain.

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A SPECIES CROSS IN CUCURBITA

THOMAS W. WHITAKER*

OVER a period of years a number of theories with respect to the wild ancestors of *Cucurbita maxima* Duch. have been proposed. Parodi,[5] and later Millán,[3] and Whitaker and Carter[7] have suggested that *C. andreana* Naud., the small, wild, bitter gourd of Northern Argentina and Uruguay, might be the ancestral type of the cultivated species. With the purpose of testing this idea experimentally, a number of reciprocal pollinations were made between the two species *C. andreana* and *C. maxima*.

Cucurbita maxima is exceedingly variable in vine and fruit characteristics. It includes such diverse forms as Buttercup (a turban type), the Hubbard group, the Banana group, and the giant-fruited Mammoth variety. The species is even more variable in South America (Northern Argentina and Chile). Millán[4] as a result of studies with the *maximas* of that area has separated out three distinct botanical varieties of the species: *zapallito*, a dwarf form; *zipinka*, a dwarf form with small, ridged fruit; and *triloba*, a dwarf form with three locules.

Contardi[2] has obtained hybrids from controlled pollinations between *C. maxima* and *C. andreana*, and has made a brief report of his results. Millán[3] has approached the problem through a study of comparative variation in *C. andreana* and *C. maxima*. He has investigated collections of *C. andreana* from a wide area in Argentina and Uruguay; and comes to the conclusion that it is undoubtedly the parent form of *C. maxima*. It is suggested that primitive agricultural peoples living in the vicinity of *C. andreana* selected out non-bitter forms for domestication. The domesticated form or forms spread with the development of agriculture, and in turn gave rise to new local forms.

The present work confirms for the most part the findings of the Latin American investigators, and presents a more detailed account of the appearance of the plants, and the genetics of the cross. Since the plants are large and considerable space is required to accumulate the numerical data required for significance in genetical experiments, the present report is confined to a description of the principal differences between the species, the characters studied, their dominance relations, and finally an estimate of the probable relationships of the two species. A report of the genetics of the several characters under investigation is reserved for a later paper.

Methods and Materials

Seed of *C. andreana* was supplied by Dr. L. H. Bailey, and the fruits grown from this seed correspond very closely to those illustrated by Bailey[1] in Figure 218. A commercial strain of *C. maxima* var. *Banana* was used as the *maxima* parent in the crosses (this variety is one of the few *maximas* which are readily grown in Southern California). Good descriptions of each species have been published (see Bailey[1] for *C. andreana*; Whitaker and Bohn[8] for *C. maxima*). The obvious similarities and differences between them are tabulated in Table I.

An attempt was made to determine the breeding reactions of *C. andreana* and four of the cultivated species. It crosses readily with *C. maxima* in both directions with the production of a fully fertile F_1 and succeeding generations (see Table II). Except for *C. maxima*, *C. andreana* in its breeding behavior seems to be more closely allied to the perennial species, *C. ficifolia* Bouché, rather than to the annual species. *C. ficifolia* is found in tropical Mexico, Central America and northern South America, usually at fairly high elevations. The fruits are relatively large, mottled green, with a hard shell, and coarse stringy flesh. Normal fruits were obtained when pollen of *C. ficifolia*, was applied to the stigmas of *C. andreana*. However, the seed, while abundant, was flat and mostly empty, except for small aborted embryos. In one fruit there were several plump seeds, but these failed to germinate. Contardi[2] obtained three fruits from twelve pollinations of the same cross, but the fruits contained only empty seed coats. Because of the peculiar length-of-day relationships of *C. ficifolia*, production of androecia is delayed until late summer. For this reason, the reciprocal cross (*C. ficifolia* × *C. andreana*) has not been tried.

Limited data suggest that *C. andreana* and *C. moschata* Duch. are incompatible. Contardi's[2] work, combined with the results of the present investigation, indicate that the same is true of the cross *C. andreana* × *C. pepo* L.

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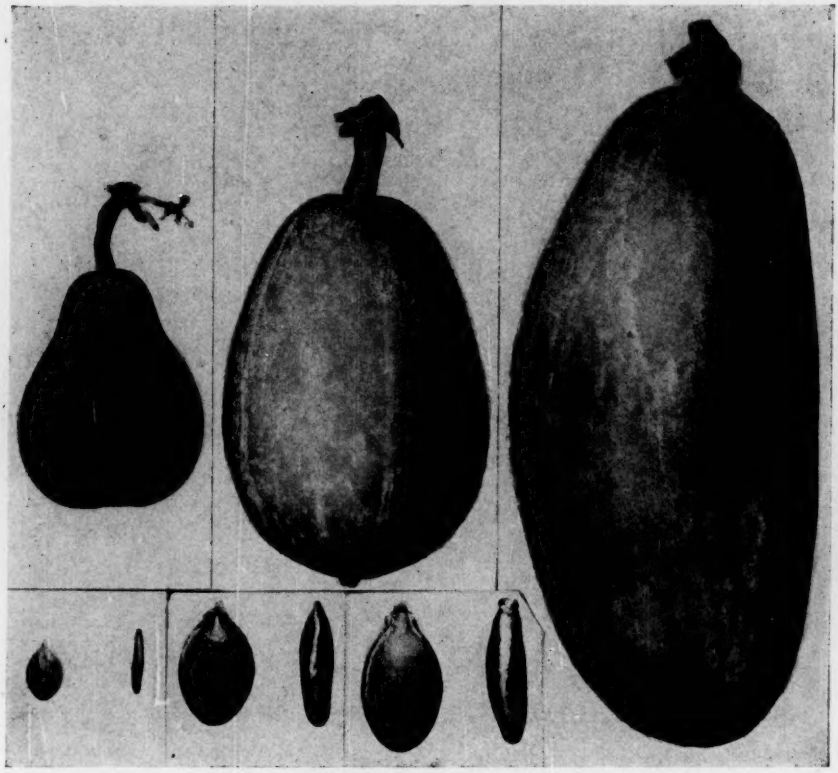


PARENT SPECIES AND HYBRIDS

Figure 5

Fruits and seeds of the parental species *Cucurbita andreana* is shown at left, of the first generation hybrid in the center, and of *C. maxima* var. *Banana* on the right. Seeds are approximately natural size and the fruits approximately one-half natural size. In the F_2 independent segregation of genes for fruit size and fruit shape was observed (see Figure 6).

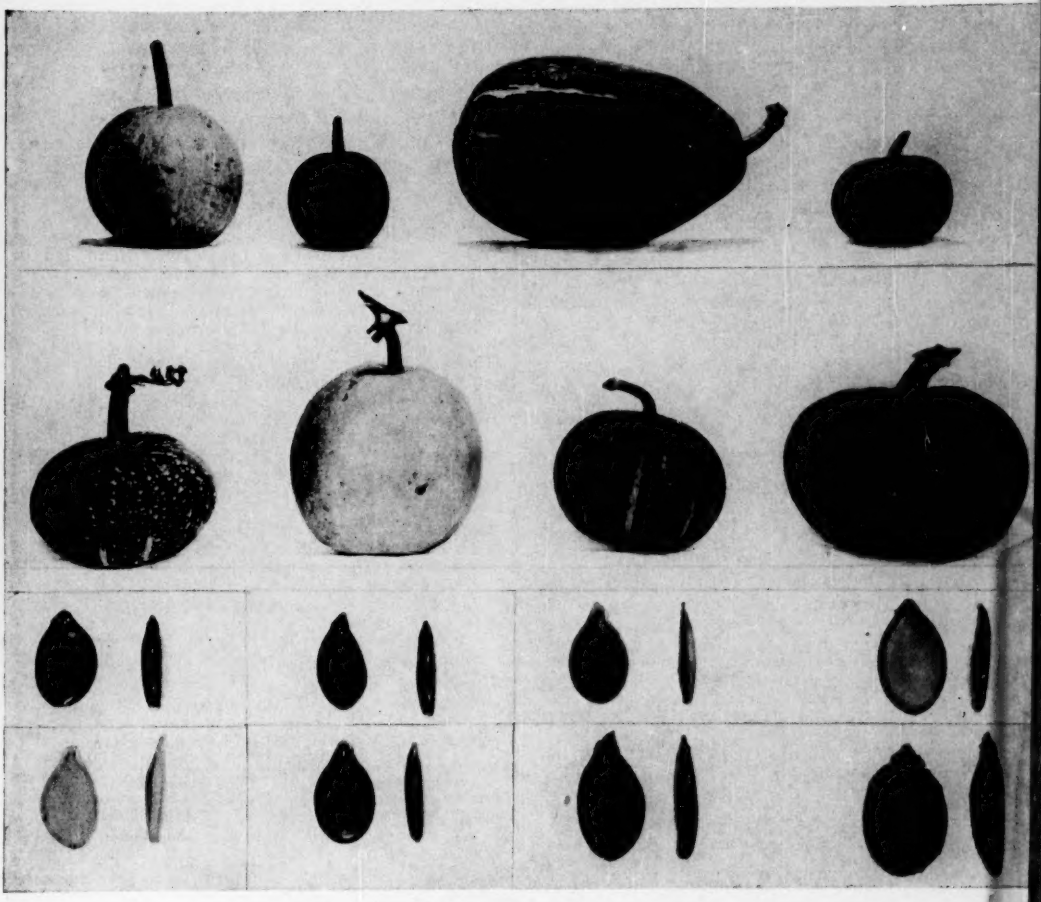
The F_1 Progeny

First generation hybrid plants from matings between *C. maxima* var. *Banana* × *C. andreana* appeared to be approximately intermediate between the two species in most vegetative characters, except for vine growth (see Figure 5). The F_1 plants had much more vegetative vigor than *C. andreana*. However, they did not equal *C. maxima* in this respect, if size of leaves and length of runners are used as criteria. For characters of a quantative nature associated with the reproductive structures such as flower size, peduncle size, fruit size, mature fruit color pattern, and seed size, the expression in F_1 was intermediate between the two parents. (See Figure 5.)

Table III lists the characters studied together with their expression in the parent species and the F_1 hybrid. It is evident that the dominant mutations are present in the wild type (*C. andreana*) and the domesticated type (*C. maxima*) in about equal numbers. It is also evident from our preliminary observations of the segregations in F_2 and F_3 families (see Figure 6)that most of these characters are dependent upon single major genes with perhaps a few modifiers in some cases.

Discussion

The important differences between these two species from a horticultural



SEGREGATION FOR FRUIT SIZE AND SHAPE

Figure 6

The eight fruits shown above are F_2 segregates from the cross of *Cucurbita andreana* and *C. maxima*. Below the fruits are shown the seeds of the eight fruits. The seeds are about natural size. The fruits are about one-quarter natural size. Note that there is no close correlation between fruit size and seed size.

standpoint are the bitter principle that controls the taste of the fruit and the hard, woody durable shell. Both dominant characters are found in the wild type and are governed by single gene mutations. The bitter principle, colocynthin,* has been extracted by Paulsen.[6] Morphologically the hard, durable rind or shell is made up of short, thick-walled stone cells, arranged in a layer of vary-

*An alkaloid principle which has a violent purgative effect. It is thought that colocynthin, formerly believed to be a glycoside, is a mixture of an alkaloid and a crystallizable alcohol, citrullol.

ing thickness, immediately underneath the epidermis. With age and desiccation this layer becomes very tough and woody and is not subject to decay through the action of micro-organisms.

There is good evidence that introgressive hybridization between the two species has occurred and takes place whenever plants of these two entities are located in the same vicinity. Contardi[2] has found that the percentage of natural crossing may be as high as 23 percent. The same author has also shown that the so-called "amargo zapallo" of the province of Cordoba is a product of natural crossing between these two species. The Zapallito de Tronco described by Bailey[1] as *C. maxima* var. *zapallito* is evidently derived from the same source.

The writer has grown and studied a collection labeled "Joko largo" from Santa Cruz, Bolivia, and another from the same locality named "Joko redondo" (collections made available through the courtesy of Dr. Hugh Cutler, Chicago Museum of Natural History, Chicago, Illinois). Both collections are undoubtedly hybrids from crosses between *C. andreana* and *C. maxima*, since they were almost identical in all respects with certain segregates of the F_2, F_3, and backcross progenies from known crosses between these species.

TABLE I. A comparison of the morpholoical similarities and differences of *C. andreana* and *C. maxima*.

Character	*C. andreana*	*C. maxima* var. *Banana*
Growth habit	annual	annual
Plant type	vine	vine
Leaves:		
Shape	rotund-reniform not lobed	cordate, reniform, not (or shallowly) lobed
Size	15-18cm broad; mid-vein 14-15 cm long	22-25cm broad; mid-vein 10-11 cm long
Margin	serrate	serrate
White spots	present	absent
Setae	long, moderately stiff	short, fairly stiff
Pubescence	extremely hairy	moderately hairy
Flowers:		
Length (♀)	7-8cm	12-14cm
Length (♂)	3.5-4cm	7-8cm
Anther:		
Length	0.7-1.0cm	1.3-1.7cm
Sepals:		
Shape	awl shaped, narrow linear	awl shaped, narrow linear
Length (♀)	3-5cm	2.5cm
Peduncles	hard, angled, small (1.0-1.5cm in di.)	corky, round, large (3.0-3.5cm in di.)
Fruits:		
Color	green, with whitish irregular strips and spots	yellow or orange-yellow
Shell	hard, durable	soft, non-durable
Shape	mostly oblong-pyriform	oblong, cylindrical
Size	8-16cm long	45-55cm long
Flesh	thin, stringy, bitter, whitish	thick, smooth, sweet orange-yellow
Seeds:		
Length	0.6-0.9cm	1.6-1.8cm
Color	grayish white	dark brown
Margin	narrow	broad

Summary

Reciprocal matings of *C. andreana* and *C. maxima* var. *Banana* have resulted in fertile F_1, F_2, and F_3 progenies. Dominant mutations are distributed fairly evenly between the two species. The major differences between these entities are evidently dependent upon single gene mutations, with perhaps modifiers in some instances. There is evidence that introgressive hybridization between the cultivated species *C. maxima* and the wild species *C. andreana* has been taking place continuously since historic times in Argentina, Uruguay, and Bolivia. The evidence with respect to the origin of these species suggests two alternatives: (a) *C. maxima* may have been derived by selection from *C. andreana*; (b) *C. andreana* may have been a weedy by-product or non-horticultural form of *C. maxima*. Millán's observations indicate that there is considerable variation in both species so that either alternative could have been exploited to produce the end result.

Aside from *C. maxima*, *C. andreana* crosses more readily with the perennial species, *C. ficifolia*, than with the other annual species used in these experiments.

TABLE II. Results of attempted interspecific crosses with *C. andreana*.

Species	No. of pollinations	Results	Seed
C. andreana × *C. maxima*	6	6 mature fruit	abundant, fertile
C. maxima × *C. andreana*	6	6 mature fruit	abundant, fertile
C. andreana × *C. ficifolia*	3	2 mature fruit	abundant, but mostly with small aborted embryos.
C. moschata × *C. andreana*	3	*no set	.....
C. andreana × *C. pepo*	4	no set	.....
C. pepo × *C. andreana*	5	no set	.....

*One fruit apparently set, then decayed while very young.

TABLE III. Characters and expression in parent species and F_1.

Character	*C. andreana*		F_1	*C. maxima* var. *Banana*
Leaf spotting	D*	present	present	absent
Peduncle	D	hard non-corky	hard, non-corky	soft, corky
Fruit epidermis	D	smooth	smooth	glaucous
Fruit flesh (taste)	D	bitter	bitter	sweet
Sex of 1st flower	r	♀	♂	♂
Immature fruit color	r	green	yellow	yellow
Fruit shape	r	necked	non-necked	non-necked
Fruit durability	r	hard	soft	soft
Seed coat color	r	white	light brown	lt. brown

*D = dominant; r = recessive.

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COMMUNIST BIOLOGY IN PEKING AND MOSCOW

THE arrival of the propaganda film "Michurin" in China (see Figure 1) quickly followed an announcement in the Chinese Communist press that "officially approved Soviet theories of heredity are to form the basis for teaching in Communist China." The Communist daily *Ta Kung Pao* of Shanghai stated in December 1949 (as reported ni the New York *Times*) that:

"Reactionary theories on heredity propounded by Mendel, Weissmann and Morgan have already been deleted from biology textbooks for the senior and middle schools but the progressive theory of Michurin should simultaneously be inserted to take the place of the discarded ones.

"In dealing with the origin of human thought and knowledge it is necessary to set forth in detail the theories of Pavlov. In dealing with Darwin's theory of evolution care should be taken to differentiate between its progressive and reactionary features.

"In dealing with Einstein's theory of relativity attention should be centered on those aspects in support of dialectical materialism while the backward aspects of the theory should be refuted. Special efforts should be made to eradicate the reactionary theories of Eddington and Heisenberg, which, as a product of Einstein's theory of relativity, have pervaded the scientific circles of the Western World."

Chinese geneticists have been forced to accept the Marxist theory of biology or leave. Those who accept Marxist biology are subjected to a course of indoctrination lasting over two years. After that they are put on probation, and any evidence of "deviationism" is likely to lead to the gravest consequences. Those who elect to return and embrace Communist principles are subject to this course of re-education. But it should not be forgotten that Soviet citizens, even though good Communists, were routinely sent to slave labor camps "merely because they had been out from Soviet control for a period of months or years." This is the testimony of Elinor Lipper, the star witness at the Rousset libel trial in Paris in 1950.

The predicament of Chinese trained in genetic principles in Western universities is very grave. The virtual impossibility of obtaining exchange fellowship visas adds greatly to difficulties in which Chinese scholars find themselves.

Demolition of the Cell

In the Soviet Union proper the great event of 1950 was the demolition of the cell as the basic unit of life. This was announced in June. A Moscow broadcast on June 7, 1950 said in part:

"A large-scale scientific conference recently took place in Moscow in the USSR Academy of Sciences. The conference was devoted to a debate on problems connected with noncell forms of life and the origin of cells. At this meeting, at which approximately 150 biologists headed by Academicians Lysenko, Oparin, Speransky, and Anichkov were present, the great discovery made by the Soviet biologist Lepeshinskaya was considered to have been scientifically proved.

"For many hundreds of years scientists the world over tried unsuccessfully to solve the problem of the origin of live matter from dead matter. Until quite recently the so-called cell theory of the German reactionary scientist Virchow had reigned for approximately 100 years in the biological science.

"Virchow maintained that there was no life in a noncell. Reactionary scientists assumed that the secret emergence of live tissues cannot be discovered, because this would have meant the undermining of religious teachings to the effect that life originated from God.

Cells from Noncell Matter

"In 1933 Prof. Q. B. Lepeshinskaya spoke for the first time against the Virchow dogma. By means of complicated experiments she proved that a cell can emerge not only from a cell but also from a live noncell matter, which, on its part, is formed from dead matter.

"At the recently held meeting leading Soviet scientists acquainted themselves with hundreds of preparations of Professor Lepeshinskaya and her methods of work.

"Today the Presidium of the USSR Academy of Sciences heard and debated the results of this meeting and the scientific discussion

which was held for a lengthy period in connection with the discoveries of Professor Lepeshinskaya.

"Academician Oparin stated: 'Virchow's cell dogma is not in accordance with reality. This lying reactionary theory is contrary to progressive Michurin biology and hinders the development of true science. The work of Professor Lepeshinskaya has opened a new stage in the development of biology and scientific teachings on the origin of life."

Revision of Teaching

"Academician Vavilov, President of the USSR Academy of Sciences, noted the very great scientific import of the work of Professor Lepeshinskaya.

"The Presidium of the USSR Academy of Sciences decreed to recommend to all biological and chemical establishments of the Academy to work on a large scale on problems of noncell forms of life, the development of cells, and on questions as to the origin of life.

"The Presidium of the Academy has approached the USSR Ministries of Higher Education and Health with the request to alter curricula and textbooks on biology, histology, pathophysiology, and other branches in order to remove remnants of idealistic presentations from teachings on cells and the origin of live matter."

The "Academician Vavilov" mentioned in the dispatch is Sergei Vavilov, brother of Nikolai Vavilov, the geneticist. Dispatches from Moscow on January 26, 1951 announced Sergei Vavilov's death. The Moscow announcement featured the fact that, like his brother Nikolai, Sergei had never become a member of the Communist party. It is thus an especially sardonic footnote to the story of the brothers Vavilov that in the last three years of his life Sergei—as President of the Soviet Academy of Sciences—was destined to promulgate the official announcements which erased the work of his famous brother from the culture of the U.S.S.R. In the 1948 decrees wherein the Soviet Academy of Sciences purged Soviet institutes of "Western rottenness" in biology and directed the rewriting of the textbooks along Michurinist lines the gene was banished from the Communist world. Then, shortly before his death, Sergei's decree abolishing the cell completed the Communist retreat to mediaevalism in biology.—R.C.

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SCIENCE IN HUNGARY

The "Underground Railroad" for "Cosmopolitans"

THE *Hungarian Bulletin* is published twice a month to keep the foreign press informed of developments in that country. The *Bulletin* for March 16 brings the western world up to date on the Congress of the Hungarian Working People's Party held in March. In a two hour speech Deputy General Secretary Jozsef Revai had some interesting remarks regarding science in Hungary. What he had to say about "two types of scientists" is noteworthy because it appears that there is a tendency on the part of scientists to escape from the blessings of the "great work in our people's cultural progress" now going on in that country.

Said Comrade Revai:

"We owe gratitude and thanks to those of our scientists who have realized, and are proving with their work, that serving science means to serve the people, the homeland and Socialism. . .

"The approach science makes towards the people, its taking a practical turn, cannot be deep and consistent enough if we fail to make aware our research workers and scientists of the two opposing poles, the patriotic scientist and the cosmopolitan scientist. . . We, in Hungary, too, have these two types of scientists. Albert Szentgyörgyi, the Nobel-prize winning physician-biologist, who years ago left his country and sold his world fame as a trademark to an American chemical trust, typifies the cosmopolitan scientist. He deserted and denied not only his country and Hungarian science, but commissioned by the imperialists, he was in fact willing to lure scientists abroad, to organize the escape of a number of Hnugarian research workers from the country.

"I could mention Pál Gombás as an example of the other type of scientist. Two years ago, he, too, misled by the cajoling of Albert Szentgyörgyi, left his country and went to America. There in the treadmill of American science, they tried to force him to do trifling things. But the scientist and the patriot was awakened in Pál Gombás. He turned for help and pardon to the Government of our People's Republic. He was granted both. We are convinced that Albert Szentgyörgyi, who sold his scientific salvation to the devil of American big capital, will lose by this deal not only as a man and a patriot, but also as a scientist. Pál Gombás, on the other hand, having found the path to his people, will do great things as a scientist, too."

One wonders. If Miss Lipper is right, Pál Gombás may find it necessary to do more great things while he is being "reindoctrinated" in a slave labor camp. "Cosmopolitan" Szentgyörgyi should really be ashamed of himself if that should happen.

THE "VESTIGIAL TAIL" MOUSE

A New Recessive Mutation

W. E. HESTON

National Cancer Institute, National Institutes of Health, Public Health Service, Bethesda, Maryland

A NEW character, vestigial tail, arose in 1947, in the colony of strain C_{57} brown mice (*Mus musculus*) maintained in the genetics laboratories at the National Cancer Institute. Three out of four females mated to their litter-mate male in the 67th brother × sister inbred generation of the strain gave birth to 65 progeny of which eight females and four males had vestigial tails. The fourth female had 17 offspring none of which showed the character. Neither of the parent females nor the male displayed the character nor had it been observed previously in the strain. Subsequently occurrence has been limited in the strain to the descendants of the three females.

Sib matings from the litters in which the character appeared in the 68th generation produced 24 vestigial-tailed mice in a total of 111. Twenty-nine, 11 of which had vestigial tails, were progeny of vestigial-tailed females × normal litter mate males; and 82, 13 of which had vestigial tails were from normal females × normal litter mate males. No offspring were obtained from the two matings in which the male was vestigial-tailed, and four of six vestigial-tailed females mated to normal males were sterile. Owing to this reduced fertility of the vestigial-tailed animals and to the emphasis placed at this time on outcrossing for segregation studies, the character was lost in the inbred line in the subsequent generation. It has been maintined in the descendants of the outcrosses.

Description of the Character

The term "vestigial tail" was chosen because it describes the character very well (Figures 7 and 8). The rudiment of the tail is usually 1 cm. or less in length although expression of the character may vary from practically no tail to one approximately one-half normal length. A slight filament indicating a resorbing process such as occurs in certain other tailless mutants is sometimes observed.*

In cleared and stained skeletal preparations† the tail was observed as terminating in a rudiment of fused, irregular vertebrae. In some individuals the fused portion was preceded by several normal appearing caudal vertebrae whereas in the extremely short tails the fused stub was adjacent to the sacral vertebrae. The remainder of the vertebral column appeared unaffected, and no other skeletal variations were found.

The affected young did not appear anemic as do flexed-tailed young nor was there observed to be any external variation associated with the character.

Segregation of the Character

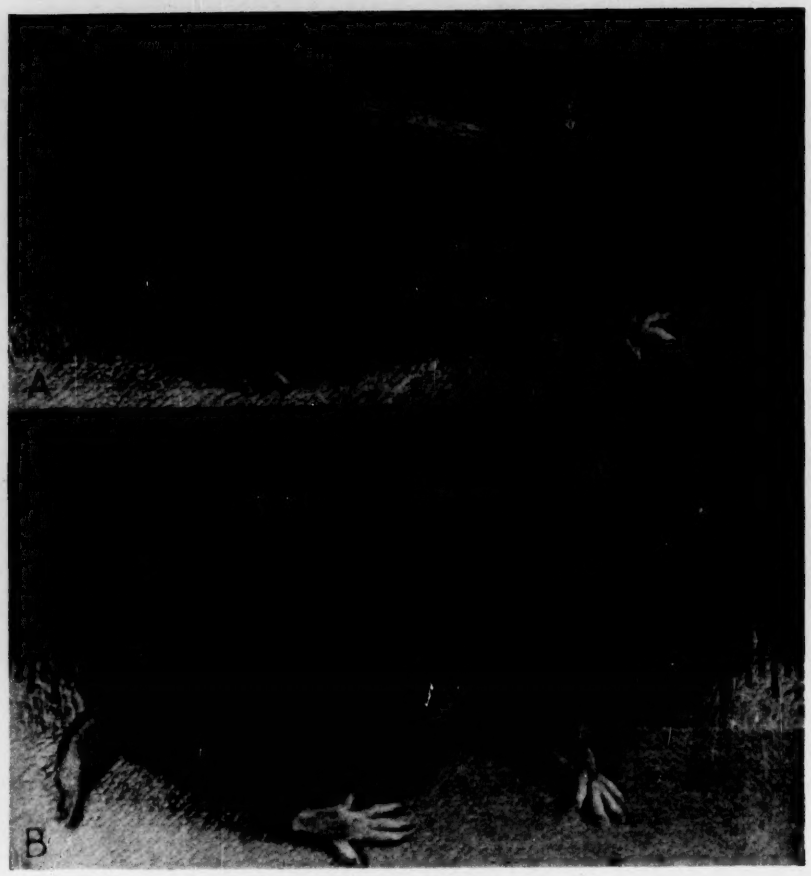
Outcrosses were made to strain *A* in order to observe segregation ratios (see Table I). Of eight vestigial-tailed C_{57} brown females mated to *A* males, three produced 3 litters with a total of 19 offspring all of which had normal tails. The remaining 5 females were apparently sterile. Later 6 C_{57} br AF_3 vestigial-tailed females were mated to *A* males and four of these females were fertile, producing seven litters totaling 58 mice, all normal. Thus, recessive inheritance was indicated.

Six $F_1 \times F_1$ matings produced a total of 36 litters consisting of 261 normal and 83 vestigial-tailed offspring. This does not differ significantly from the ratio of 258:86 expected with single factor segregation ($X^2 = .14$; $P = .70$).

Of the eighteen F_1 vestigial backcross matings made, 12 were fertile, producing 19 litters with a total of 135 young. The ratio of 76 normal to 59 vestigial-tailed did not fit the

*Dunn, L. C.: Some relations between mutations and abnormal development. Roscoe B. Jackson Memorial Laboratory Twentieth Commemoration lectures on genetics, cancer, growth, and social behavior. Printed by the Bar Harbor Times. pp. 79-91 (1949).

†The skeletons were prepared for study by Wayne D. Levillain.



VESTIGIAL TAILED MICE

Figure 7

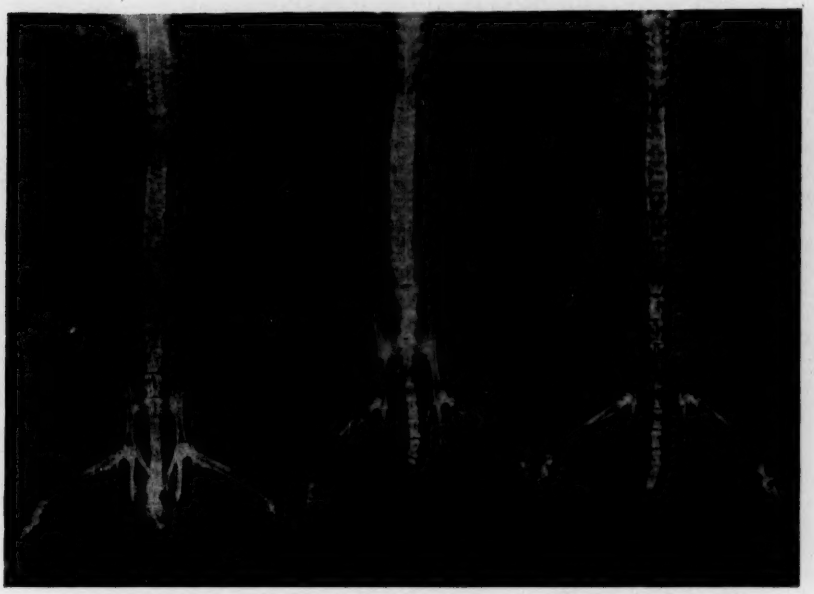
Two adult vestigial tailed mice are shown to illustrate the degree of variation of the character. Extreme vestigials have practically no tail at all. Some of them boast tails half normal length.

expected single factor ratio (64.5:64.5) as well as did the F_2 ratio, but the difference was not significant ($X^2 = 2.14$, P is between .10 and .20).

Two vestigial-tailed F_2 males used in these $F_1 \times$ vestigial matings were fertile, while a vestigial-tailed F_2 male was sterile. Seven of the 10 vestigial-tailed females used in these backcross matings were shown to be fertile while the remaining three were mated to the same F_1 male that was not proved to be fertile.

From 13 fertile vestigial $\times$ vestigial matings (F_2, F_3 and backcross vestigial-tailed segregants) 45 litters with a total of 357 offspring were obtained. All of these were vestigial-tailed.

Breeding tests of six normal backcross segregants (4♀ and 2♂) were made by mating to vestigial-tailed mice. From the first backcross female, seven litters were obtained containing 38 normal and 33 vestigial-tailed offspring; from the second, one litter with 4 nor-



DEVELOPMENT OF CAUDAL VERTEBRAE IN SHORT TAILED MICE

Figure 8

Some tails, almost half normal length have over a dozen vertebrae, while extreme "tailless" mice have a knob of fused vertebrae at the end of the spinal column.

mal and 4 vestigial-tailed; from the third, one litter with 5 normal and 4 vestigial-tailed; and from the fourth, one litter with 4 normal and 4 vestigial-tailed. From one normal backcross male segregant, five litters with 19 normal and 17 vestigial-tailed offspring were produced; and from the other, 4 litters with 12 normal and 20 vestigial-tailed. These matings yielded a total of 82 normal and 82 vestigial-tailed offspring: in exact agreement with expectation.

The results of the various progeny tests of the normal and vestigial-tailed backcross segregants, and of F_2 and F_3 segregants, make it apparent that the character is controlled by a single recessive autosomal gene with full penatrance. No lethal effect was indicated by the segregation ratios or litter size from the various types of matings. The character appeared to be distinct from all other tail mutants although tests for linkage with the other tail mutants have not yet been made. The name vestigial tail with the symbol *vt* is therefore applied, such designation to be withdrawn if the character is later shown to be an allele of one of those already described.

The two parent strains used in these studies differed in respect to the albino

TABLE I. — Segregation resulting from outcrossing vestigal-tailed strain C_{57} brown mice to normal-tailed strain *A*.

Type of Mating	Offspring	
	Vestigial-tailed	Normal-tailed
Vestigial × normal *A*	0	77
F_1 × F_1	83	261
F_1 × vestigial	59	76
Normal-tailed backcross segregants × vestigial	82	82
Vestigial × vestigial	357	0

TABLE II. — F_2 generation mice segregated as to genotype with respect to albinism and vestigial tail.

Genotype	Number	
	♂	♀
C– Vt–	73	77
C– vt vt	25	16
c c Vt–	21	25
c c vt vt	10	10

gene, thus providing a test for linkage to this gene. From Table II it can be observed that the distribution of the phenotypes recorded at weaning time in the F_2 generation did not differ significantly from that expected with random assortment ($X^2 = 2.38$, with 3 degrees of freedom, P is approximately .5).

While the data of Table I were gathered from the young at birth and were not separated as to sex, the data in Table II were tabulated at weaning age and separated according to sex with no indication of a sex difference.

Summary

A new mutation designated as vestigial tail appeared in the 68th brother × sister inbred generation of strain C_{57} brown mice. The tail was usually less than 1 cm. in length with approximately one-half normal length the extreme variation, and was terminated in fused, irregular vertebrae. No other variations were observed to be associated with the character.

Single recessive autosomal factor inheritance with full penetrance was indicated by the segregation ratios from outcrossing vestigial-tailed mice to normal strain A, and was confirmed by breeding tests of the backcross, F_2 and F_3 segregants. The symbol vt was therefore applied.

Vestigial tail is not linked with albinism.

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The Hemophilia Foundation

The Hemophilia Foundation, a philanthropic organization, was chartered by the State of New York in January 1949.

The chief purpose of the Foundation is to render direct aid to indigent sufferers. The extent of such aid is governed entirely by the financial resources of the Foundation.

A secondary purpose is to sponsor and encourage research in Hemophilia.

The ultimate purpose of the Foundation is to establish its own center for rehabilitation and useful education of boys and men with Hemophilia. Plans for such an institution are being considered and will come into being at a future time.

Any person is eligible for membership in the Foundation upon application and payment of annual dues of $5.00. The Foundation is primarily one of parents and close friends of parents. Sufferers are automatically made members without payment of dues.

Hemophilia is an hereditary disease caused by the lack of coagulation of the blood, transmitted by mothers to sons only.* It is one of the oldest known diseases, mentioned in the Old Testament. The "bleeders" disease known for thousands of years . . . is older than Christianity, itself. Rasputin was reputed to be able to prevent (probably based on hypnotism) hemmorhaging in hemophiliacs which, in part, explains his hold over the Czars of Russia in his day. If so, the secret died with Rasputin.

The Foundation estimates that there are about 40,000 cases of the disease in the United States.

Robert Lee Henry is President of the Foundation which maintains an office at 60 East 42nd Street, New York 17, New York. Literature may be obtained by addressing the Foundation, which is anxious to register the name of every known hemophiliac in this country.

—*Amer. Assoc. Mental Deficiency News*, Oct.-Dec., 1950

*Unfortunately not true. On the average, "carrier" women transmit the hemophilia gene to half their sons and to half their daughters, who are in their turn "carriers." In those rare cases when a hemophiliac male survives he transmits his hemophilia-bearing X-chromosomes to all his daughters, but to none of his sons.—Ed.

INTERSPECIES HYBRIDS IN PINES

A Summary of Interspecific Crossings in the Genus *Pinus* Made at the Institute of Forest Genetics

F. I. Righter and J. W. Duffield*

PRECOCIOUS OFFSPRING

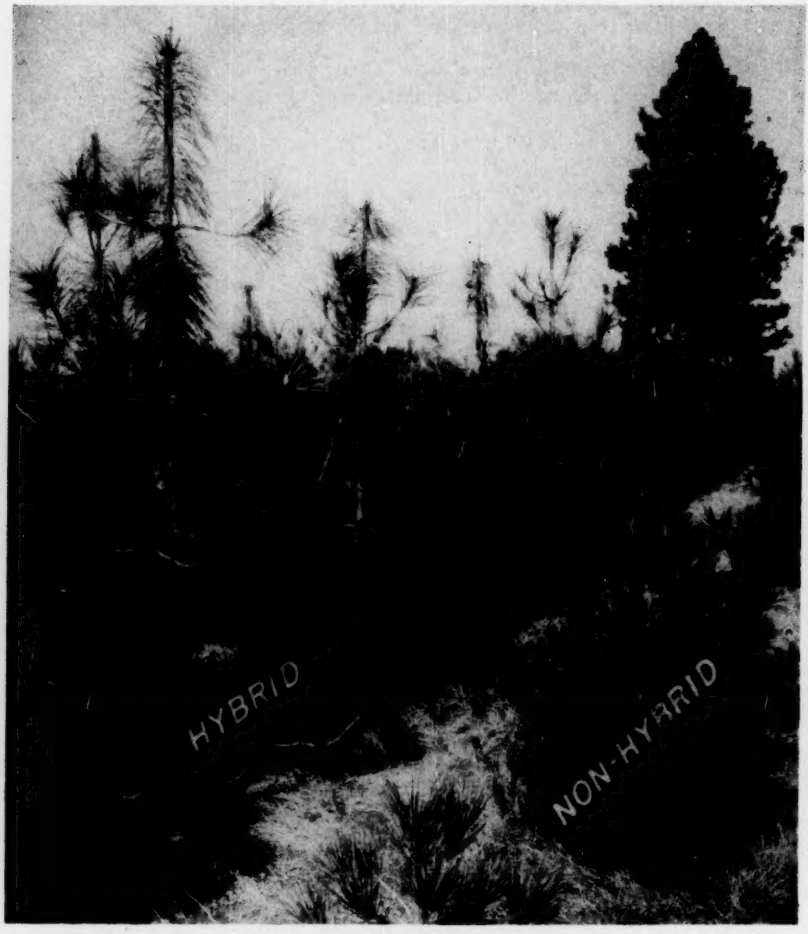
Figure 9

The growth of seedlings of a hybrid between *Pinus attenuata* and *P. remorata* are compared with those of the parent species. The seedlings shown are all two years old. The front row and the second row show the two parent species, *P. remorata* and *P. attenuata*. The tops of the seedlings are connected with strings. The back row shows the growth of the first generation hybrid between these two species. This is one of several blocks of randomized plots used to establish the statistical significance of differences in growth rates.

SINCE 1926, when the Eddy Tree Breeding Station—now the Institute of Forest Genetics—started its program of species crossing in *Pinus*,[1] approximately 230 interpollinations between species have been attempted. Of these attempted hybridizations, 46, including some inter-varietal crossings and backcrossings of hybrids, have thus far yielded viable progeny. Most of these have been obtained since 1939. This article summarizes these results, leaving detailed descriptions of the various hybrids to papers published,[10, 12] in preparation, and projected.

Cumming and Righter[4] have presented

*Forest Geneticists, at the Institute of Forest Genetics, California Forest and Range Experiment Station, which is maintained by the Forest Service, U. S. Department of Agriculture, in cooperation with the University of California, Berkeley, Calif.



BACKCROSS AND PARENT COMPARED

Figure 10

This photo shows a 't' test of the backcross of a hybrid with one of the parent species. The row on the left shows ten year old plants of *P. jeffreyi* × (*P. jeffreyi* × *P. coulteri*). The row labelled "non-hybrid" is planted to ten year old seedlings of *P. jeffreyi*. The hybrids consistently show much greater vigor than the parent *jeffreyi*.

the techniques used in obtaining most of the hybrids recorded herein. Liddicoet and Kimbrough have described[5] the practices employed in propagating them. These techniques, because of their refinements, greatly facilitate early recognition of hybrids as such. In general, this has been accomplished by sowing the putative hybrid population in nursery rows adjacent to rows sown to the open-pollinated population from the same seed tree. Such sowings, usually

laid out as "t" tests, facilitate early estimation of the magnitude of developmental and morphological differences between juvenile populations, particularly if the percent of non-hybrids in hybrid plots is low. Usually, few non-hybrids are found when effective pollination techniques are properly applied.

TABLE I. *Pinus* species hybrids made at the Institute of Forest Genetics, and date of first successful pollination.

Parents (Species or hybrids)			
Seed parent	Pollen parent	Date	Remarks, references to literature, etc.
attenuata Lemm.	*radiata* D. Don	'27	Hybrid, which also occurs in nature, has been named × *P. attenuradiata.*[12] Cross repeated 1947.
attenuata Lemm.	*remorata* Mason	'46	
attenuata Lemm.	*muricata* D. Don	'47	
attenuata Lemm.	*attenuradiata* Stockwell & Righter	'34	Cross repeated.
attenuradiata Stockwell & Righter	*attenuata* Lemm.	'34	
attenuradiata Stockwell & Righter	*radiata* D. Don	'34	
contorta Dougl.	*banksiana* Lamb.	'46	
contorta Dougl.	*contorta* var. *latifolia* Engelm.	'47	
contorta var. *latifolia* Engelm.	*banksiana* Lamb.	'39	Hybrid, which also occurs in nature[6] has been named × *P. murraybanksiana.*[10] Possible case of heterosis.[2] Cross repeated several times.
contorta var. *latifolia* Engelm.	*murraybanksiana* Righter & Stockwell	'47	
echinata Mill	*caribaea* Morelet	'31	
echinata Mill	*glabra* Walt.	'46	All hybrids somewhat chlorophyll deficient, and died during first season.
echinata Mill	*rigida* Mill	'41	Hybrids involving these species have long been known.
echinata Mill	*taeda* L.	'33	Cross repeated many times.
echinata Mill	*echinata* × *caribaea*	'45	Cross repeated 1946.
echinata Mill	*echinata* × *taeda*	'45	Cross repeated 1946.
flexilis James	*griffithi* McClell.	'47	
griffithi McClell	*strobus* L.	'47	Possible case of heterosis.
jeffreyi Grev & Balf.	*coulteri* D. Don	'44	Natural hybrids occur. Cross repeated 1946.
jeffreyi Grev & Balf.	*ponderosa* Laws.	'31	Hybrids involving these species have long been known. Cross repeated several times.
jeffreyi Grev & Balf.	*jeffreyi* × *coulteri*	'39	Pollen obtained from a natural hybrid.[8, 2] Cross repeated many times.
jeffreyi × *ponderosa*	*latifolia* Sarg.	'47	Seed parent is natural hybrid.
lambertiana Dougl.	*armandi* Franch	'47	Stone and Duffield.[13]
lambertiana Dougl.	*koraiensis* Sieb & Zucc.	'47	Stone and Duffield.[13]
monticola Dougl.	*strobus* L.	'39	Cross repeated many times. Possible case of heterosis.[8]
monticola Dougl.	*griffithi* McClell.	'42	Cross repeated several times.
monticola Dougl.	*ayacahuite* Ehren.	'46	
monticola Dougl.	*peuce* Griseb.	'47	
monticola Dougl.	*peuce* × *strobus*	'46	Pollen sent from Denmark by C. Syrach-Larsen.
murraybanksiana Righter & Stockwell	*contorta* var. *latifolia* Engelm.	'47	
murraybanksiana Righter & Stockwell	*banksiana* Lamb.	'45	
nigra var. *calabrica* Schneid.	*nigra* var. *austriaca* Asch. & Graeb.	'42	
ponderosa Laws.	*ponderosa* var. *scopulorum* Engelm.	'41	Cross repeated many times.
ponderosa Laws.	*latifolia* Sarg.	'43	Cross repeated 1946, 1947.
ponderosa Laws.	*ponderosa* var. *arizonica* (Engelm.) Shaw	'46	Cross repeated.
ponderosa Laws.	*montezumae* Lamb.	'46	
ponderosa var. *arizonica* (Engelm.) Shaw	*ponderosa* Laws.	'42	
ponderosa Laws.	*washoensis* Mason & Stockwell	'46	
ponderosa var. *scopulorum* Engelm.	*ponderosa* Laws.	'41	
remorata Mason	*radiata* D. Don	'42	
rigida Mill	*taeda* L.	'33	Cross repeated in 1941.
rigida Mill	*rigida* × *taeda*	'42	
sondereggeri H. H. Chapm.	*taeda* L.	'45	Seed parent is natural hybrid *palustris* Mill × *taeda* L.
strobus L.	*griffithi* McClell.	'40	Possible case of heterosis.
taeda L.	*caribaea Morelet*	'31	
taeda L.	*echinata* × *taeda*	'45	
washoensis Mason & Stockwell	*ponderosa* Laws.	'41	

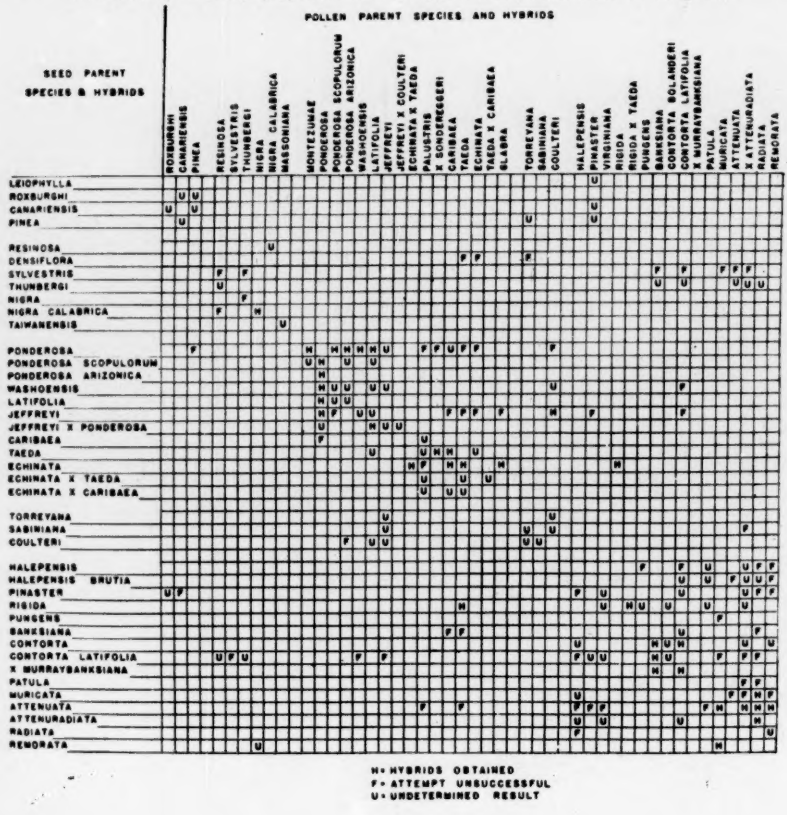
Method of Detecting Hybrids

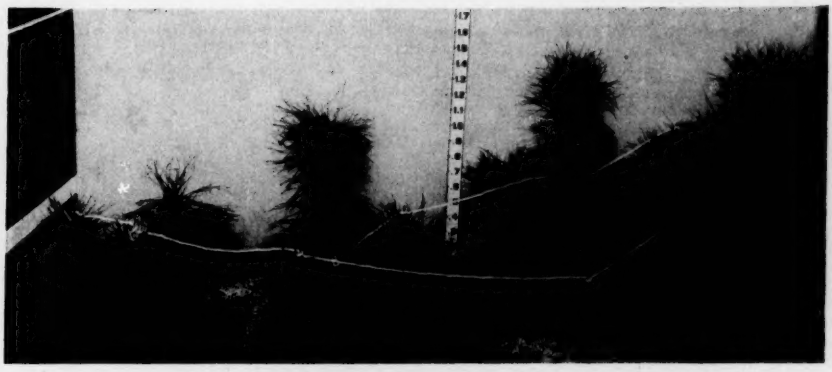
One characteristic tested in this way is germination behavior. All seeds are subjected to a standard stratification treatment, and this results in decreasing the variability of germination behavior within a population. In many cases, then, it is possible to distinguish populations characterized by different mean germination times.[8] Thus, if a single tree produces two populations of seed differing significantly in germination behavior, and this difference is associated with difference in pollen parentage, the presumed pedigrees of the two populations are provisionally confirmed. Another feature of young pine seedlings which may be related to pollen parentage is the age at which short shoots first appear.[13] Thus, in several instances, hybrid populations have been distinguished from non-hybrid populations from the same seed tree on the basis of first-year or second-year production of such shoots. Other features which have been helpful in this respect are color and length of foliage, number of needles per fascicle, color of terminal shoots, type of bud, and rate of growth. (See Figure 12.)

Summary of the Program

The hybrids obtained from pollinations through 1947 are listed in Table I. Three hybrids reported in earlier publications[7] as having been obtained at the Institute of Forest Genetics (*P. ponderosa* × *P. mugo*, *P. ponderosa* × *P. sabiniana*, and *P. coulteri* × *P. ponderosa*) have not been obtained. Rather, Austin[1] reported that seed had been obtained from the first two crosses given above. Subsequent investigation showed, however, that the seeds were not hybrids, but *P. ponderosa* which resulted from imperfect pollination-con-

TABLE II. Status of species crossing in the section Haploxylon Koehne of the genus *Pinus*. This summarizes the successful, unsuccessful, undetermined and untried crosses in this section of the genus.

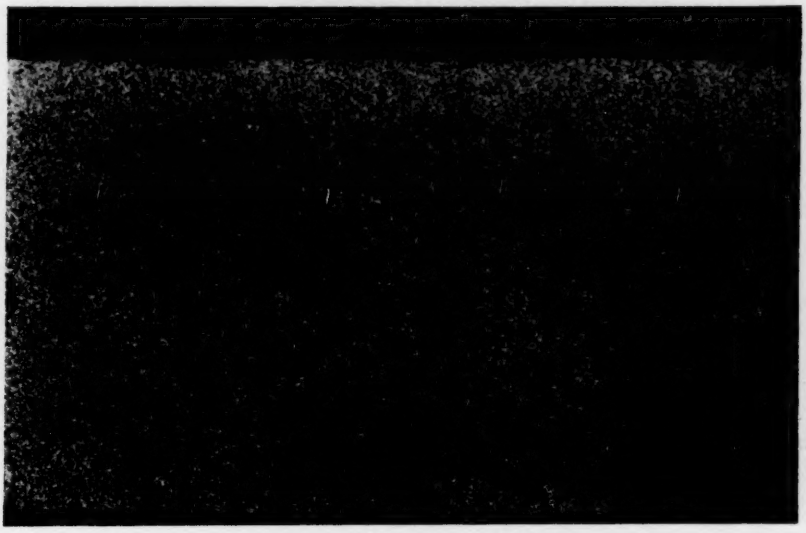




HYBRID VIGOR IN INTRASPECIES CROSS

Figure 11

The parents of this test are *Pinus contorta* var. *latifolia* (first row) and *Pinus contorta* (second row). The seedlings of the two parent species are connected by strings. In the third row are seedlings of hybrids between these two sub-species. All seedlings are two years old.



SUPERIOR GERMINATION OF HYBRID SEED

Figure 12

The rows designated by "H" are planted to seeds of the hybrid *Pinus monticola* × *P. strobus*. The other rows show germination of open pollinated seed from the same seed tree which produced the hybrid seed. The photograph was taken three weeks after sowing.

trol technique. No record of the third crossing exists.

Attempted hybridizations that failed have an interest to systematics almost as great as the successes. Tables II and III are presented to show the results of the entire program: the hybrids made, the crossings which have failed, and those which because of inadequacy of data, or recency of the attempts, cannot yet be classified. Since few inter-sectional crosses have been attempted and none has been successful, the two sections of the genus, *Haploxylon* and *Diploxylon* are dealt with in separate tables. In each table, the arrangement of species follows in general Shaw's[11] classification of the genus into relationship groups.

Only the "H" entries in these tables represent final conclusions respecting the crossability of species between which crossings have been attempted. Since it is obviously impossible to prove that no pair of individuals belonging to two species can be successfully crossed, the "F" entries in the tables merely indicate a likelihood that the species are not crossable. Where many attempts have been made, the likelihood that the cross cannot be made is considered high; where fewer attempts have been made and the parent species are believed, on other grounds, to be closely related, the "F" entries are subject to revision following further experimentation. Tables II and III do not indicate the numbers of attempts involving each species combination. This obviously limits the value of the "F" entries in determining relationship groups. As the species-crossing program progresses, repetitions of successful and unsuccessful attempts are made as opportunities arise. It is planned, as adequate data are accumulated, to use these as an aid to the taxonomic revision of the genus *Pinus*.

The practical purpose of the crossing program is to produce promising hybrids for extensive testing in forest plantings according to the procedure outlined by Righter[9] or by other methods specially devised for testing particular characters. During the spring of 1950, on five national forests in California, approximately 15,000 hybrid transplants from controlled pollinations were interplanted with similar open-pollinated stock of *P. ponderosa* and *P. jeffreyi* the principal species used for reforestation in California. The hybrids represented in these plantings are: *P. ponderosa* × *P. ponderosa* var. *scopulorum*, *P. ponderosa* × *P. ponderosa* var. *arizonica*, *P. ponderosa* × *P. latifolia*, and *P. jeffreyi* × (*P. jeffreyi* × *P. coulteri*). These plantings were part of a program of world-wide cooperative testing of pine hybrids produced at the Institute of Forest Genetics.

TABLE III. Species crossing in the section Diploxylon Koehne of the genus *Pinus*.

SEED PARENT SPECIES & HYBRIDS	POLLEN PARENT SPECIES & HYBRIDS: KORAIENSIS	CEMBRA	ALBICAULIS	FLEXILIS	ARMANDI	AYACAHUITE	LAMBERTIANA	PARVIFLORA	PEUCE	PEUCE × STROBUS	STROBUS	GRIFFITHI	MONTICOLA	MONOPHYLLA	BALFOURIANA	ARISTATA
ALBICAULIS	F	F														
FLEXILIS				U		U						F	H			
ARMANDI			U										U			
AYACAHUITE																
LAMBERTIANA	H		F		H	F		F	F		F	F	F			F
STROBUS					F		F						H	U		
STROBUS × GRIFFITHI													U	U		
GRIFFITHI			U			F					U		U			
MONTICOLA	U			U	H	F	U	U	H	H	H					F
CEMBROIDES														U		
EDULIS														U		
BUNGEANA											F					
BALFOURIANA			U									F				U
ARISTATA			U									F			U	

H = HYBRIDS OBTAINED
F = ATTEMPT UNSUCCESSFUL
U = UNDETERMINED RESULT

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A GOAT WITH HETERONYMOUS HORNS

H. EPSTEIN*

CLOCKWISE AND COUNTERCLOCKWISE

Figure 13

An ordinary corkscrew has a right-handed spiral, as does the right horn of nearly all the spiral-horned breeds of goats. The left horn spirals in the opposite direction. The single female goat in this group—the small black individual in the center of the picture—has such homonymously spiralled horns. All the other goats shown are males from Kurdistan; and all of them have horns spiralled in the opposite direction. This rare deviation is found in goats from the high plateaus of southwest Asia, as far West as Kurdistan. The spiral of the horns of homonymous breeds is often eliminated by castration, but this is not the case with the heteronymously spiralled forms.

AN ordinary screw or corkscrew represents a right-handed spiral. In following the ridge on such a spiral from base to apex we pass continuously to the right.[10]

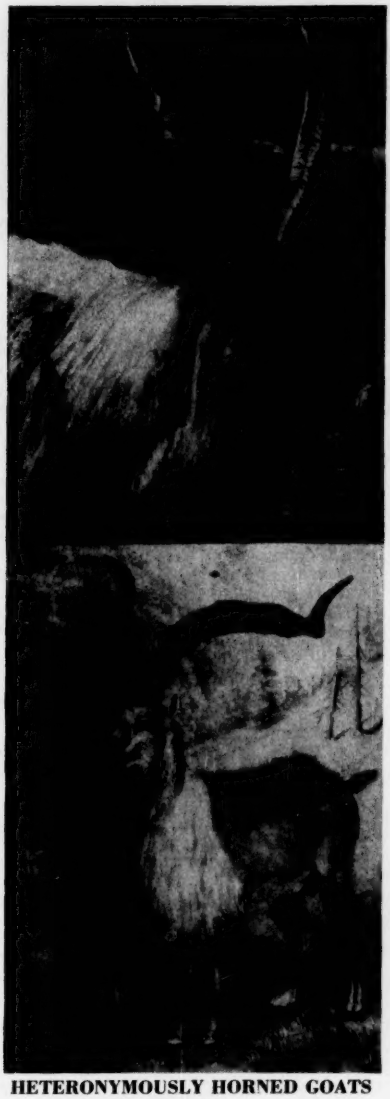
The condition wherein the right horn forms a right-handed spiral and the left horn a left-handed spiral is termed homonymous. In contrast to this is the heteronymous condition in which the right horn forms a left-handed spiral and the left horn spirals to the right. The heteronymous condition obtains in wild goats as represented by *Capra falconeri*. But all domesticated goat breeds, with one exception, are homonymous.

*This note is condensed from a chapter of Dr. Epstein's forthcoming book, "The Origin of the Domestic Animals of Africa." The entire chapter, containing many additional photographs and measurements of the Kurdish goats described has been published as a supplementary document. To obtain a copy of this chapter, order Document 3255 from American Documentation Institute, 1719 N St. NW, Washington 6, D. C., remitting $1.00 for microfilm images 1 inch high on standard 35 mm. motion picture film) or $2.70 for photocopies (6×8 inches) readable without optical aid.

ANCIENT AND MODERN GOATS

Figure 14

A—Statuette, "Ram of the Goats" from the royal graves of Ur, about 3500-3200 B. C. (after Wooley). The screw-like homonymously spiralled horns of fifty-five centuries ago are to be compared with a modern Iraq goat shown at *B*. *C*—is a bronze head of a homonymously horned goat from the Bronze Age of the upper Kukan about 3000 B. C. (after Antonius). *D*—is a bronze statuette from Karak, Mesopotamia dated about 3000 B. C. (after Meissner).



HETERONYMOUSLY HORNED GOATS

Figure 15

A shows a detail of the head and neck of a modern Kurdish goat showing open heteronymous spiral. Below is shown the Markhor, *Capra falconeri falconeri* (after Lydekker). This species occurs in Afghanistan and Baluchistan and may be the progenitor of the heteronymously horned Kurdish goats.

Several students of palaeozoology[3,6,8,11] hold that the screw-horned goats of ancient Egypt and Mesopotamia were heteronymously horned descendents of the markhor. Adametz[1] goes even further, maintaining that the Suleman subspecies of the markhor is the ancestral stock of the Egyptian and Mesopotamian screw-horned (strepsiceros) goats. Referring to this type of goat on an Assyrian relief from the palace of Sennacherib, Adametz says: "Every zoologist immediately recognizes in this picture the subspecies of the markhor known as the *Capra falconeri jerdoni*." This theory, however, has not remained unchallenged. Binder[5] and Augst[4] have independently pointed out that in the large majority of domesticated strepsiceros goats the spiral runs in the reverse direction to that in the markhor, the first turn of the front ridge of the horns inclining inwards.

The strepsiceros goats of ancient Egype belong also to this homonymous group. Hilzheimer[7] describes the horns of a skull from Abusir-el-Meleq as of 'prisca' type, that is homonymous. Additional evidence is provided by the ancient Mesopotamian screw-horned goats which, although distinguished by a longer pelage, are of the same racial type as the goats of ancient Egypt. Their horns are homonymous, as shown by the bronze head of a goat from Rarah and the statuette of a 'Ram of the Goats' from Ur. The same strepsiceros breed occurred in ancient Syria, Asia Minor, and the Indus valley.

In short, all strepsiceros goats of ancient Asia and Africa appear to have been homonymously horned; this likewise applies to the recent strepsiceros goats sporadically found in Europe and Africa, in addition to those occurring in Asia, with but one exception.

This exceptional breed is first mentioned by Lydekker,[9,10] who refers to it as the Circassian, but does not provide any description beyond the statement that it is the only breed of tame goats with heteronymous horns. A photograph of a male specimen of this breed, kept at one time in the Cairo Zoological Garden, is produced by Antonius,[3] who also calls it "Circassian,' but gives no further information apart from a reference to its heteronymous horns. Hilzheimer[7] mentions that this breed has a very restricted distributional area. Amschler,[2] however, ascertained in the northern Caucasus that none of the Circassian tribes possessed such goats, all their flocks consisting of animals carrying powerful horns of the homonymous type.

Nor does evidence exist that heteronymously horned goats were known in the northern part of the Caucasus in ancient times. The bronze head of a goat from the late bronze age of the Upper Kuban, worn apparently as an amulet, shows homonymous horns, and not the heteronymously horned breed occurring in other parts of the Caucasus.

Domesticated goats with heteronymous horns were found by Amschler[2] in Daghestan, in the Oset Autonomous Area and in the Shiraki steppe of Transcaucasia, as well as in the steppe of Kosh Agatch, in the Central Altai, where they occur in large flocks. Amschler claims that the distributional area of this type comprises parts of the Caucasus, Persia, Afghanistan, northern India and the Asian high plateau with its folded border ranges. Lydekker[9] states that in Himalaya it is by no means uncommon to see domesticated goats having spiral horns of the markhor type; and Blanford mentions a Nepalese goat skull with heteronymous horns in the British Museum.

Heteronymous Goats from Kurdistan

In 1942-44, as Technical Adviser (Meat) to the Food Controller, Government of Palestine, the present author had the opportunity of handling many thousands of goats brought into Palestine from the north. The great majority was of the small black Iraqui breed distinguished by twisted or screw-like homonymous horns; very few specimens had scimitar-shaped horns or were polled.

However, among flocks of a thousand or so there always were two or three goats totally different from the rest. They were large animals, almost twice the weight of the Iraqui stock, with very long silky hair and long heteronymous horns. Although the Government contractors were bound to supply animals of Turkish origin only, it was an open secret that the majority of their goats purchased in the north-eastern corner of Syria were smuggled in from Iraq, with only a few coming from Turkey. All inquiries in connection with the heteronymously horned goats elicited the reply that they came from Kurdistan, which thus appears to be the westernmost limit of the range of this breed.

While the majority of the Iraq goats supplied were females, the Kurdish goats were, with no exception, males, so that the following description applies only to the latter sex. The contractors asserted that sometimes flocks of five hundred or more animals of this type were offered them with not a single female amongst them, so loath were the Kurds to part with their female stock. The female is said to be somewhat smaller than the male, and her horns are shorter and thinner, but otherwise of the same twist and direction as the male horn.

It is impossible to determine the geographical race of *Capra falconeri* to which the ancestry of the heteronymously horned domestic goats may be traced. This is not only because of the considerable variation in the shape and direction of the horns of the domestic breed. Had there been even a higher degree of uniformity in horn shape and direction, this would not necessarily provide a clue in the quest of the local variety of markhor from which the domesticated stock might be descended. In view of the far-reaching effects of domestication, there can be no doubt that the heteronymous turn in the horns of the domestic breed may have been derived from any of the local races of *Capra falconeri*, and that the variations in the shape and direction of the horns met with in the heteronymously horned domesticated goats are merely a result of domestication, and not in every instance of a fixed inheritance from a different ancestrial race.

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CYTOGENETIC STUDIES ON BUCKWHEAT*

Genetic and Cytological Studies of Compatibility in Relation to Heterostyly in Common Buckwheat, *Fagopyrum sagittatum*†

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THE common species of buckwheat, *Fagopyrum sagittatum*, belongs to the group of plants known as heterostyled which have different forms of flowers, based primarily on the reciprocal relationship between the height of the styles and of the stamens. Buckwheat has two kinds of plants: the one having flowers with short styles and long stamens, and the other having flowers with long styles and short stamens. A close relationship exists between the heteromorphic condition and the compatibility of sexual unions. In compatible unions the stamens and styles concerned stand at the same height, while in incompatible unions the stamens and styles stand at different levels.

This paper reports the results of some experiments which were made on buckwheat to observe the amount of difference in seed set between the compatible and incompatible combinations. Cytological studies were also made to compare the behavior of the pollen tubes in the styles after compatible and incompatible matings.

Review of Literature

Darwin[1] and Korshinsky and Monteverde[4] found that controlled crosses in buckwheat of long × short or short × long gave more seed than crosses of long × long or short × short. Garber and Quisenberry[2] observed that selfed short-styled plants set more seed than selfed long-styled.

In cytological studies on *Fagopyrum sagittatum* Stevens[7] found that in compatible combinations a three-celled proembryo had developed 18 hours after pollination, while in incompatible combinations the pollen tubes took more than 72 hours to reach the ovary. Schoch-Bodmer[5] observed that after compatible matings the pollen tubes reached the base of the short style in 5 to 15 minutes and of the long style in 15 to 20 minutes. She found that, in the incompatible matings, the pollen tubes at first grew almost as fast as in compatible matings, but that after 15 minutes their growth was slowed down and after two to three hours almost completely stopped. In the long styles the pollen tubes were checked when they had traversed two-thirds of the style, while in the short styles they were checked in the region where the stigma merges into the style. In her early work[5] Schoch-Bodmer believed that inhibiting substances were at work in incompatible matings. Further experiments[6] led her to believe that the incompatibility could be explained by an exhaustion of some growth substance in the long styles or by an inability of the pollen tubes to penetrate the more compact tissue of the short styles.

Material and Methods

In order to compare the results of compatible and incompatible combinations two experiments were set up, the first in the greenhouse in August 1944, and the second in the field during the summer of 1945. Since it was realized that the most accurate way to test the differences was to use the same plant or genotype for all the possible combinations of selfing and crossing, this was accomplished by the use of cuttings in the 1944 experiment, and by the use of different branches on the same plant in the 1945 experiment. For the 1944 experiment the open-pollinated Japanese variety of buckwheat was used, while the plants in the 1945 experiment were the progeny of four compatible combinations in the 1944 test.

Controlled pollinations were made by covering the plants with cheesecloth cages and individual branches with cheesecloth sleeves. In the greenhouse the plants were set in a moist chamber on the previous evening to keep the pollen from shedding when the flowers opened the next day. Emasculations were made in the early morning with a forceps and binocular-

*Paper No. 247, Department of Plant Breeding, Cornell University, Ithaca, New York. The research reported herewith is part of a thesis submitted to fulfill in part the requirements for the degree of Doctor of Philosophy.

†Cited by Hill[3] as the correct scientific name for common buckwheat since it has priority of date (1792) over *Fagopyrum esculentum* Moench. (1794).

loupe or an electric suction pump. Selfing was accomplished by a fine camel's hair brush thoroughly coated with pollen and brushed lightly over the stigmas. Crosses were made by applying to the stigma an individual stamen or flower held with the forceps. In the field the flowers to be used as males were collected in gelatin capsules.

The plants used for cytological studies were grown in the greenhouse during the summer of 1946 and pollinations were made during August and the first part of September. During treatment the plants were set under fluorescent lights in a laboratory where the temperature range was from 68° to 76° F. They received 12 hours of light per day as long as they remained in the laboratory.

At definite intervals of time after controlled pollinations had been made, the flowers were fixed in three parts of absolute alcohol and one part of glacial acetic acid for 24 to 36 hours, then stored in 70 percent alcohol. For clearing and staining the flowers were transferred from 70 percent alcohol to hot lactophenol for three minutes in the case of short-styled flowers and two minutes in the case of long-styled flowers. They were next placed on a glass slide and the styles dissected from the ovary and the rest of the flower. The styles were placed in a hot solution of one percent acid fuchsin in lactophenol for ten minutes in the case of short styles and for fifteen to twenty minutes in the case of long styles. They were then transferred to lactophenol and after ten minutes were mounted in lactophenol. The slides were examined with a 10× ocular and a 16mm. objective. An ocular micrometer was used for measuring the styles and a green filter improved differentiation of the tubes within the styles.

Results and Discussion

Genetic Studies

A summary of the results of compatible and incompatible combinations for the combined experiments is presented in Table I and the results of testing the same genotype in all possible combinations for the 1945 experiment are set forth in Table II.* In each case the data show that there are highly significant differences between selfings and incompatible crosses or between the crosses long × short or short × long (Student's "t" test for unpaired observations).

From these tables it is evident that the incompatibility in *Fagopyrum sagittatum* is not complete. On the other hand the same plant shows marked differences in seed set from different mating combinations. In both the compatible and incompatible combinations there is a considerable amount of aborted seed, as high as 50 percent of the total set in some cases. Since this holds true for the 1944 experiment in the greenhouse and the 1945 experiment in the field, it would appear that some inherent factor rather than the environmental condition caused the abortion.

POLLEN TUBE GROWTH IN COMPATIBLE MATINGS

Figure 16

Photomicrographs of styles after compatible matings. *A*—Long × short, 20 minutes after pollination. *B*—Short × long, 2½ hours after pollination. Note in both cases the dark pollen grains, which have germinated recently, and the colorless grains emptied of their contents. (Magnified 40×.)

*Eight additional tables are available as a supplementary document. To obtain this material, order Document No. 3215 from American Documentation Institute, 1719 N. Street, NW, Washington 6, D. C., remitting $1.00 for microfilm or for 6 × 8 inch photocopies.

INCOMPATIBLE POLLINATION

Figure 17

Photomicrographs of styles after incompatible pollinations. *A*—Short × long, 60 hours after pollination. Note penetration of one tube into style. *B*—Long × long, 72 hours after pollination. The tubes have penetrated slightly over half the stigma and style. *C*—Long × long, 10½ hours after pollination. Some tubes have burst near the base of the style. (Magnified 40×).

Cytological Studies

In all the mating combinations observed cytologically, out of a total of 2742 pollen grains observed on the stigmas, only 57 had failed to germinate. This shows that the incompatibility of certain matings is not due to failure of the pollen to germinate.

In the combinations short × long and long × short the pollen tubes reached the base of the styles within 15 minutes after pollination (Figure 16). The observations were not sufficient to show whether the tubes of long-styled pollen traversed the short styles (.66 mm. average length) more rapidly than the tubes of short-styled pollen traversed the long styles (1.47 mm. average length), as Schoch-Bodmer found from her work. Only one burst pollen tube out of 500 was noticed in these combinations.

In the incompatible combinations the selfings and the crossing of like-styles gave the same behavior for short and long styles, respectively. In the combinations short × short and short selfed, the pollen grains germinated within 10 minutes, and within 20 minutes most of the tubes had grown through the stigmatic tissue to the point where the stigma merged into the style. At this point a checking oc-

TABLE I.—Results of compatible and incompatible combinations among all the plants of the combined tests for 1944 and 1945.

	Total Number				Per Cent	
Plant combination and style length	Flowers pollinated	Swollen ovaries	Normal seed	Aborted seed	Nor. and abt. seed	Normal seed
long selfed	3243	94	36	55	2.8	1.1
short selfed	3184	183	120	63	5.7	3.8
long × long	1486	47	30	17	3.2	2.0
short × short	732	40	20	20	5.5	2.7
long × short	1372	759	465	294	55.3	33.9
short × long	995	600	328	272	60.3	33.0

TABLE II.—Results of testing in all possible combinations four genotypes in the 1945 progeny of the 1944 experiments.

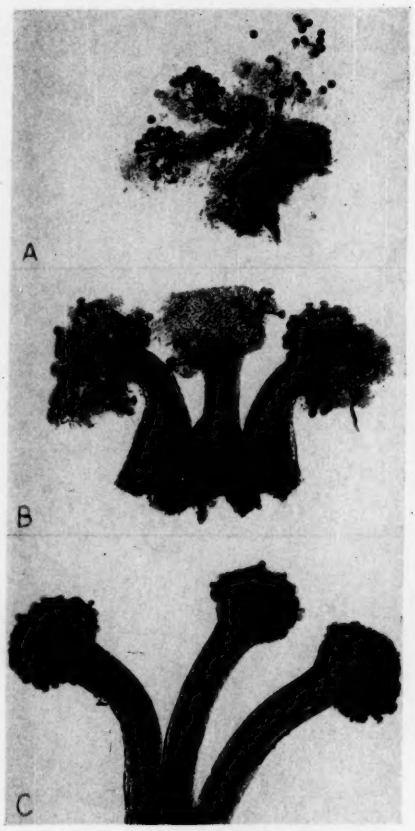
	Total Number				Per Cent	
Plant combination and style length	Flowers pollinated	Swollen ovaries	Normal seed	Aborted seed	Nor. and abt. seed	Normal seed
1. The four genotypes selfed:						
A. 18 (14) long	1646	30	0	30	1.8	0
B. 18 (17) long	694	38	18	20	5.5	2.6
C. 18 (15) short	1912	79	57	22	4.1	3.0
D. 18 (16) short	775	43	34	9	5.5	4.4
Average					4.2	2.5
2. Cross combinations:						
A × B	89	2	0	2	2.2	0
B × A	97	3	0	3	3.1	0
C × D	92	7	1	6	7.6	1.1
D × C	86	3	2	1	3.5	2.3
Average					4.1	0.8
A × C	89	74	40	34	83.1	44.9
A × D	82	28	7	21	34.1	8.5
B × C	80	39	20	19	48.7	25.0
B × D	33	31	17	14	93.9	51.5
Average					64.9	32.5
C × A	110	73	43	30	66.4	39.1
C × B	104	48	16	32	46.2	15.4
D × A	97	81	52	29	83.5	53.6
D × B	97	73	49	24	75.3	50.5
Average					67.8	39.6

curred and for the next 72 hours no or very little growth took place (Figure 17*A*). In a short style selfed, after 48 hours one tube had reached the base of the style and the ovary had begun to swell. This was an exception to the general behavior. At the end of 72 hours the stigmas and styles were showing signs of deterioration.

In the combinations long × long and long selfed, pollen germination took place within five to ten minutes, and within 20 minutes from one-half to three-fifths of the stigma and style had been penetrated. The pollen tubes grew very little beyond this point, and the maximum distance penetrated during 72 hours was three-quarters to four-fifths of the stigma and style (Figure 17*B* and *C*). In one case of long selfed, five hours after pollination, two pollen tubes were observed at the base of the styles.

In the incompatible matings of both long and short styles a number of burst pollen tubes was noted. In the short styles the burst tubes were in the stigmatic tissue, whereas in the long styles the burst tubes were in the stigma and in different parts of the style down to the point at which growth was checked.

The results agree closely with the behavior observed by Schoch-Bodmer. The problem is to find an explanation for the checking of growth in the incompatible matings. Since some seed set was obtained from incompatible combinations, a few pollen tubes must succeed in reaching the ovary to effect fertilization. Pollen from short-styled plants produces thicker pollen tubes than pollen from long- styled plants. Schoch-Bodmer suggested that the checking of pollen tubes in incompatible matings might be mechanical, due to the more compact tissue of the short style or the greater distance to be traversed in the long style. In this case it is possible that in short styles an occasional pollen tube could become thin enough to penetrate the tissue, while in the long styles some pollen tubes might possess a greater reserve of growth substances which would enable them to reach the base of the style. However, the fact that most of the pollen tubes are checked in one specific region of both the short and long styles would tend to preclude purely mechanical causes. Since inhibition occurs at different regions in the long and short styles, it is possible that the reaction is not the same in the two forms. On the other hand, if secretions from the ovary are concerned in the inhibition, the distance from the ovary at which checking in growth occurs is approximately the same in short and long styles.



POLLEN TUBE GROWTH IN SPECIES CROSSES

Figure 18

Photomicrographs showing pollen tube growth in crosses between *Fagopyrum tataricum* and *F. sagittatum*. *A*—Pollen of *F. tataricum* on stigma of *F. sagittatum* long, 30 minutes after pollination. Pollen tubes have grown nearly to base of styles. *B*—*F. sagittatum* short × *F. tataricum*, 24 hours after pollination. (Tubes still in stigma.) *C*—*F. sagittatum* long × *F. tataricum* 12 hours after pollination. Tubes have penetrated two-thirds of style (Magnified 40×).

Cytological Studies of Pollen Tube Growth in Reciprocal Crosses Between *F. sagittatum* and *F. tataricum*

Attempts were made to cross common buckwheat, *Fagopyrum sagittatum*, and Tartary buckwheat, *Fagopyrum tataricum*, with the aim of combining in the progeny the self-compatibility of Tartary and the larger seed with looser seed-coat from common buckwheat. The two species were caged together with houseflies, but no hybrids were detected among the plants grown from the seed formed on each species. Several hundred hand pollinations were made for reciprocal crosses of the two species, using as parents two diploids, two tetraploids, or a diploid and a tetraploid. When *Fagopyrum sagittatum* was used as female parent, there was never any indication of compatibility. When *Fagopyrum tataricum* diploid was used as female, occasionally the ovary would swell until it had reached one-quarter to one-half the size of the mature fruit, at which time it would turn brown and wither. In some cases the embryos were excised before the ovaries turned brown and placed on nutrient medium in sterile bottles, but none showed more than slight development.

In attempting to find the basic cause of the incompatibility between the two species some cytological observations were made on pollen tube growth. Controlled pollinations were made for reciprocal matings of diploid *Fagopyrum tataricum* and diploid long- and short-styled *Fagopyrum sagittatum*. The cytological technique and treatment of plants were the same as described for the studies on common buckwheat.

When *F. tataricum* as female was pollinated with either long- or short-styled *F. sagittatum*, the pollen tubes reached the base of the styles within 20 minutes. There were no burst pollen tubes or any other signs of incompatibility with regard to pollen germination and pollen tube growth when the cross was made this way (Figure 18*A*).

When *F. sagittatum* short as female was crossed with *F. tataricum*, the pollen grains germinated normally and grew for a short distance into the stigmatic tissue, but seemed to be inhibited at the entrance to the stylar tissue. There was only a slight penetration into the style 58 hours after pollination. Signs of incompatibility were indicated by burst pollen tubes (Figure 18*B*).

When *F. sagittatum* long as female was crossed with *F. tataricum*, the pollen tubes penetrated about two-thirds of the stigma and style within thirty minutes. In that region they seemed to be checked from further growth and after 58 hours were still in the same position (Figure 18*C*).

It is interesting to note that the behavior of *F. tataricum* pollen tubes in the long and short styles of *F. sagittatum* is identical to the behavior of pollen tubes in incompatible matings of *F. sagittatum*. In both cases the inhibiting region is located, in the short style, at the base of the stigma and, in the long style, approximately one-third of the distance from the base of the style.

Summary

Observations on genetic and cytological studies of compatibility in relation to heterostyly in *Fagopyrum sagittatum* show that significant differences were obtained between the seed sets of compatible and incompatible matings and no significant differences between the selfings and the incompatible crosses, or between the crosses long × short and short × long. Cytological studies of pollen tube growth after different mating combinations showed that in compatible combinations the pollen tubes reached the base of the styles within 15 minutes after pollination, whereas in incompatible combinations the pollen tubes were checked at the base of the stigma in the short style and in the lower half of the long style.

A study of pollen tube growth in the interspecific cross between *Fagopyrum sagittatum* and *Fagopyrum tataricum* showed that pollen tubes of *F. sagittatum* reached the base of *F. tataricum* styles, but that pollen tubes of *F. tataricum* were inhibited in *F. sagittatum* styles.

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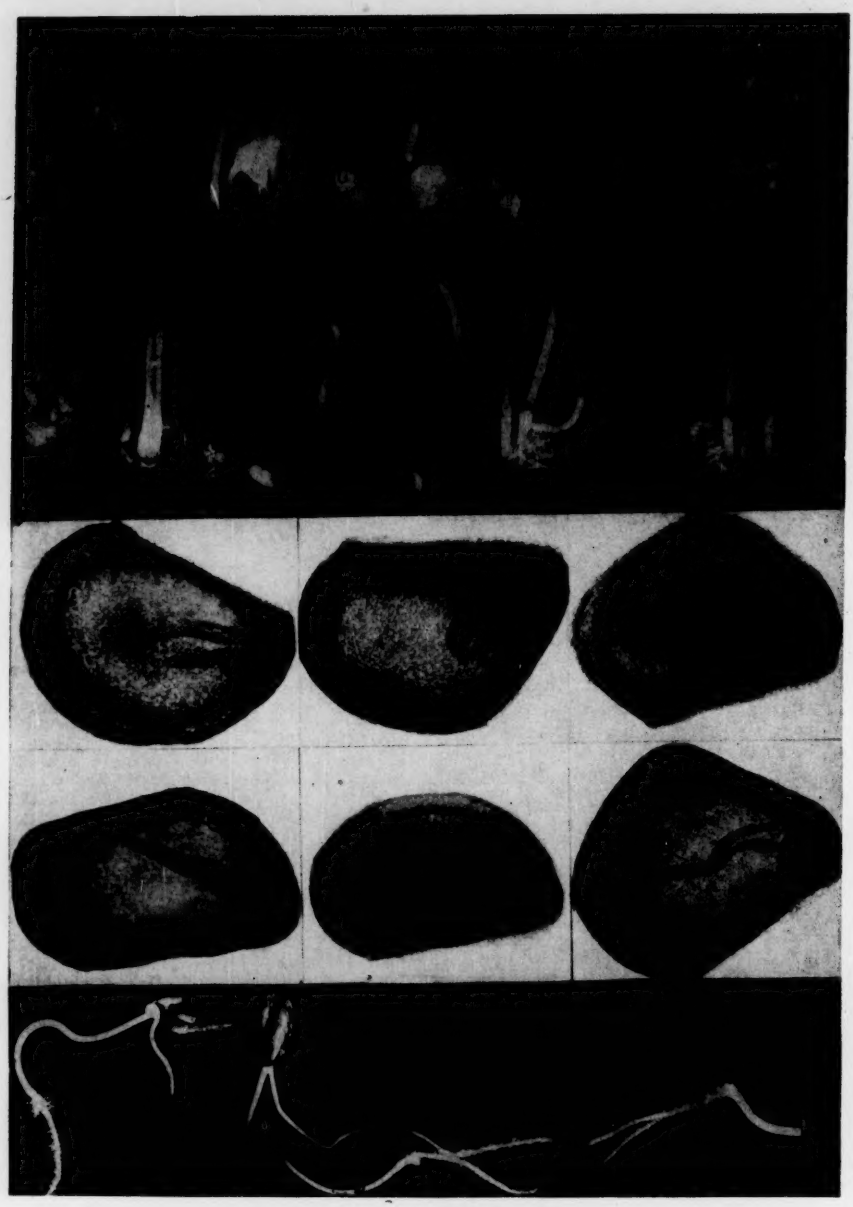

INDUCED POLYEMBRYONY

Figure 19

Polyembryonic seeds and seedlings of *Zea mays* and *Lilium regale* from crosses with X-rayed pollen. *Top row:* Unattached polyembryonic seedlings of *Zea mays*. *Second row:* The three twins of *Zea mays* on the left are partially conjoined and conjoined types. Diploid chromosome counts were obtained for all members of the three seedlings to the right (conjoined twin, unattached triplet and unattached twin). *Third and Fourth row:* Biembryonic seeds of *L. regale*. *Fifth row:* From left to right: Unattached twin seedlings of *L. regale* obtained from germination of the first seed in the fourth row; unattached twin with members of approximately the same size; partially fused twin.

POLYEMBRYONY IN MAIZE AND LILY

Following X-irradiation of the Pollen*

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POLYEMBRYONIC seeds and seedlings have been reported in many different species of higher plants. The number of seeds with two or more embryos ordinarily represents only a very small proportion of the total. In an attempt to induce a number of chromosomal aberrations in *Zea mays* and *Lilium regale* for cytogenetic studies, pollen from normal plants of these two species was exposed to several dosages of X-rays. Plants free from any detectable chromosomal aberrations were used as female parents and crossed with the irradiated pollen. Striking increases in the frequency of polyembroyonic seeds and seedlings resulting from the above crosses were observed independently by the two authors. Since it was immediately apparent that the irradiated pollen had in some manner greatly increased the proportion of polyembryonic seeds and seedlings in both *Zea mays* and *L. regale*, the results of the several X-ray dosages were recorded and are reported in this paper.

Induced Polyembyrony in *Zea Mays*

Pollen of the inbred line *KYS* was subjected to dosages of 600 *r*, 2600 *r*, and 3720 *r*, of unfiltered X-rays. Plants of the same inbred line were used as female parents and crossed with the irradiated pollen. The seeds obtained from these crosses were germinated at room temperature in a moist chamber. The number of polyembryonic seedlings observed is listed in Table I. Seeds of inbred line *KYS* resulting from crosses with pollen which had not been irradiated were germinated as a control. Numerous twin and several triplet seedlings were observed in the group resulting from crosses with irradiated pollen, while only two twin seedlings were observed in the control group. An analysis of Table I discloses that the frequency of polyembryonic seedlings increased from approximately one polyembryonic seedling among 850 seedlings in the control group to approximately one polyembryonic seedling among six germinated seeds following the X-ray dosage of 3720 *r*. The increase in frequency of polyembryonic seedlings for each of the experimental groups was statistically significant in comparison with the control. Although the majority of the polyembryonic seedlings resulting from X-ray treatment of the male gametophyte resembled the spontaneous twin seedlings, some of the induced polyembryonic seedlings were distorted in appearance. Most of the twin and triplet seedlings were unattached with the two or more members separate from one another (Figure 19). However, conjoined or partially fused twin seedlings were occasionally observed.

Many of the seeds resulting from crosses with pollen exposed to dosages of 2600 *r* and 3720 *r* were small in size and shrunken in appearance, presumably due to genetic changes induced in the male gametes and reflected in the embryo and endosperm. Moreover, the inbred line *KYS* typically produces comparatively weak seedlings. Consequently germination percentages were low for the seeds arising from crosses with pollen exposed to the higher dosages and many of the polyembryonic seedlings did not survive after early phases of growth. However, root tip chromosome counts were obtained for all members of five twins and the one triplet arising from crosses with pollen exposed to 3720 *r*. Complete chromosome counts were also obtained for four twins following 2600 *r* treatment of the pollen and for both twins in the control group. All root tip chromosome counts disclosed the diploid complement of twenty chromosomes.

Polyembryony in Seeds and Seedlings of *Lilium Regale*

Plants of *L. regale* conforming to the accepted taxonomic description of the species were grown in the greenhouse. The flower buds were emasculated and the anthers allowed to dehisce on paper towels. Pollen samples from each plant were observed to be well filled with starch and normal in appearance.

*Paper No. A309, Contribution No. 2266 of the Maryland Agricultural Experiment Station, (Department of Botany).

†The authors are indebted to Dr. Henry L. Myer and the Biophysics Department of the National Institute of Health for the irradiation of the pollen of *L. regale*. The assistance of Dr. Drew Schwartz, who irradiated the *Zea mays* pollen at Columbia University, is also gratefully acknowledged.

The pollen was exposed directly to copper and aluminum filtered X-rays at dosages of 500 *r*, 1000 *r*, 1500 *r* and 2500 *r*. Approximately 50 pollinations were made with each lot of pollen exposed to dosages of 1000 *r*, 1500 *r*, and 2500 *r*. Since the irradiation was performed with the objective of obtaining as many chromosomal aberrations as possible for cytogenetic studies, relatively few crosses were made with pollen exposed to 500*r*. Seeds from crosses made at the same time with normal pollen for other purposes were available as a control group.

Since lily seed is relatively thin, the embryos were clearly evident when examined with transmitted light and classification was readily accomplished. The number of monoembryonic and biembryonic seeds obtained in the control group and following the various pollen treatments are recorded in Table II. In comparison with the control frequency, a statistically significant increase in the frequency of biembryonic seeds occurred in each experimental group. The frequency of seeds with twin embryos was approximately 50 times as great in the group following the pollen treatment of 500 *r* as in the control group. In *L. regale* the higher X-ray dosages were less efficient in inducing polyembryony than the dosage of 500 *r*. The dosage of 2500 *r* was nearly lethal to the pollen. No twins were observed among the 16 seeds with embryos obtained from crosses with pollen exposed to 2500 *r*. Following crosses with X-ray treated pollen, increases were noted in the number of seeds with small embryos and in the number of seeds entirely lacking embryos. Some of the biembryonic seed was germinated and the resulting twin seedlings photographed (Figure 19). Three types of twins occurred among the seedlings. Twins were observed in which the two members were unattached and approximately of equal size. Unattached twin embryos were also observed in which one of the members was much smaller than the other. Finally, fused or conjoined twins were observed. Since seedlings of *L. regale* grow rather slowly it has not been possible to obtain material for chromosome counts.

Discussion

The data indicate that X-ray treatment of the pollen can cause a significant deviation from normal reproduction resulting in the formation of supernumerary embryos. Intraspecific differences in frequencies of polyembryony have been reported for several genetic lines of *Nicotiana tabaccum*,[2] *Asparagus officinalis*[8] and *Capsicum frutescens*.[6] The possibility that the differences in frequencies of polyembryony observed in the present study were due principally to genetic factors is excluded by the use of the inbred line of *Zea mays* and the magnitude of the differences between the experimental groups and the control.

Multiple embryo formation has been of considerable interest to the morphologist because it constitutes a major deviation in reproduction and embryological development. Recently polyembryony has also been of interest to the plant breeder since numerous variants in chromosome number have been observed among the plural seedlings. The haploid plants occurring among polyembryonic seedlings are of particular significance because the chromosome number of the haploids may be doubled to produce homozygous diploids.[1,4,6,7,8,9,10] Thirty different double haploids have been produced in the garden pepper, *Capsicum frutescens*.[6] The haploid member of a twin seedling is ordinarily smaller and less vigorous than the diploid. The twin seedlings having members of different sizes, as shown in Figure 19 indicate that haploids could also occur among the polyembryonic seedlings resulting from crosses with pollen exposed to X-rays. Careful control of growing conditions and the use of vigorous stock may facilitate a greater degree of survival among the smaller embryos than was obtained in the present study. A significant increase in the frequency of haploids of *Triticum monococcum* following X-ray treatment of the pollen has been reported by Katayama although no mention is made of the occurrence of polyembryonic seedlings.[5] Katayama interpreted the increased frequency of haploids as being due to the stimulation of the egg by pollen in which the male gamete had been destroyed by the X-rays.

Morgan and Rappleye in an extensive search for polyembryonic seedlings in *Capsicum frutescens* found unattached and conjoined twin and triplet seedlings.[6] Unattached and conjoined multiple seedlings were observed in the present study following X-ray treatment of the pollen of both *Zea mays* and *L. regale*. The

TABLE I. Frequencies of polyembryonic seedlings following X-irradition of the pollen of inbred line *KYS* of *Zea mays*.

Pollen dosage (*r* units)	Dormant seeds	Germinated Seeds — Seedlings — Monoembryonic	Polyembryonic Twins	Triplets	Percent Polyembryony
3720	346	126	27	1	18.18
2600	1480	704	100	3	12.76
600	587	536	9	0	1.65
0	1810	1714	2	0	0.12

TABLE II. Polyembryonic frequencies following X-irradiation of the pollen of *Lilium regale*.

Pollen dosage (*r* units)	Monoembryonic seeds	Biembryonic seeds	Percent Biembryonic seeds
2500	16	0	0.000
1500	16,332	8	0.049
1000	14,184	18	0.127
500	5,335	18	0.336
0	13,609	1	0.007

types of polyembryonic seedlings found following X-ray treatment of the pollen paralleled those occurring spontaneously in *C. frutescens*.

Since X-ray treatment of the pollen significantly increases the number of polyembryonic seedlings, the origin of the multiple embryos is of considerable interest. The mode of natural multiple embryo formation can vary for different species. Apoximis and other deviations from the normal sexual process and embryological development have been reported.[11] Cooper, in an embryological study of seven species of *Lilium* including *L. regale*, observed that a synergid was stimulated to divide in approximately one percent of the embryo sacs analyzed.[3] However, the haploid embryo ordinarily disintegrated at an early stage of development. In the present study one spontaneous biembryonic seed of *L. regale* was observed among 13,610 mature seeds from the control group. In the group of seeds developing from crosses with pollen exposed to 500 *r* units, the frequency of biembryonic seeds was increased approximately 50 times over the control. Utilizing genetic markers, Morgan and Rappleye have shown that unattached and conjoined diploid-diploid twin seedlings of *C. frutescens* were sexual in origin.[6] The conjoined pepper twins were interpreted as having originated from cleavage of the embryo during development. It seems likely that the conjoined twins observed in *Zea mays* and *L. regale* following crosses with X-rayed pollen also originated from cleavage of the embryo. In addition to examination of embryological development following pollination with irradiated pollen, experiments are in progress in which the male and female parents are genetically marked and the pollen X-rayed to determine the origin of the polyembryonic seedlings.

Summary

1. In comparison with control populations, striking increases in the number of polyembryonic seeds and seedlings of *Zea mays* and *Lilium regale* were observed resulting from crosses employing X-rayed pollen.

2. The types of multiple seedlings that occurred following irradiation of the pollen resembled spontaneous polyembryonic seedlings. Unattached and conjoined polyembryonic types were observed in both species.

3. Root tip chromosome counts were obtained for all members of one triplet and nine twin seedlings of *Zea mays* arising from crosses utilizing irradiated pollen. Chromosome counts were also obtained for the four members of the two twin seedlings from the control. All chromosome counts disclosed the diploid complement of twenty chromosomes.

4. Methods are discussed for determining the origin of the supernumerary embryos arising in crosses employing X-rayed pollen.

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A GENETIC BUD MUTATION IN THE PEAR

An orchard of Bartlett pears, owned by A. D. MacKelvie of Zillah, Washington, and planted in 1913, produces typical fruit of this variety with the exception of one small branch on one tree. A bud mutation appeared in 1938 on one of these trees as a small lateral branch approximately seven feet above the base of the tree. The remainder of this large framework branch produces typical fruit above and below the mutation.

This mutation, which has been named Max-Red Bartlett, produces reddish shoots and

leaves and dark red fruit. The young fruit develops this unusual color immediately after blooming and maintains it throughout the season. As the fruit ripens after picking the color changes to an attractive bright red color. In size, form, and flesh the fruit is typical of the Bartlett parent. Many trees have been propagated by budding, reproducing the mutation true to type.

The red color of the bark extends at least three cell layers deep below the epidermis.

I have used this mutation extensively in breeding work, and have found it to be genetic in character. That is, it will transmit its characteristics to a large percentage of its seedlings.

Before presenting the breeding results it must be stated that Bartlett and most other varieties of pears are practically self-sterile, and will seldom produce any seed unless fertilized with pollen of another variety. Hence, no selfed seedlings are available for study.

It is evident (Table I), that the parent Bartlett produces only green seedlings whether open pollinated or used as a male parent crossed with Comice. The Max-Red Bartlett from open pollinated seed produced 43.7 percent red seedlings. Max-Red Bartlett × Comice produced 56 percent red seedlings, while Comice × Max-Red Bartlett produced 54 percent red seedlings. In contrast, Comice open pollinated produced only green seedlings.

TABLE I. Breeding Results of Max-Red Bartlett.

Parentage	Total number of seedlings	Red seedlings	Green seedlings
Bartlett, open pollinated	23	00	23
Max-Red Bartlett, open pollinated	48	21	27
Max-Red Bartlett × Comice	41	23	18
Comice × Max-Red Bartlett	189	102	87
Comice × Bartlett	132	00	132
Comice, open pollinated	50	00	50

It is most evident from these results that the Max-Red Bartlett transmits the red color of the leaves and bark to a high percentage of the seedlings when used either as the female or male parent.

These seedlings are only one year old, hence none has fruited. Every effort is being made to bring them into fruiting as quickly as possible. However, since the red color of the Max-Red Bartlett fruit is correlated with the red color of the leaves and bark it is highly probable that these red seedlings will also produce red fruit.

The Max-Red Bartlett is a very vigorous grower, fully equal to Bartlett in this respect. However, most of the red seedlings of the Max-Red Bartlett are considerably smaller than the green seedlings produced by this variety and the Bartlett. Fortunately a small percentage of these red seedlings are as vigorous and as large as the green seedlings.

Since the above manuscript was prepared I have found that another red pear, which originated as a bud mutation, is also genetic. This variety, known as Royal Red Hardy, originated as a bud mutation on a Beurre Hardy tree in an orchard owned by Mr. V. A. Silvera of Milpitas, California. This mutation produces fruit entirely covered with dull red, and the young shoots, at least in the early stages of growth, have reddish bark and leaves. The Beurre Hardy parent produces greenish-yellow fruit with green leaves and bark.

I now have numerous young seedlings (from open pollinated seed) of both the parent Beurre Hardy and the mutation. All the Beurre Hardy seedlings have green leaves and stems, while forty-two percent of the Royal Red Hardy seedlings have red bark and reddish leaves.

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SYMPOSIUM ON GENES AND MUTATIONS

THE Long Island Biological Laboratory at Cold Spring Harbor is sponsoring a symposium on quantitative biology devoted to a searching discussion of the nature of the gene, its evolution, and of the mechanism of mutation. The symposium runs from June 7 through June 15. Introductory periods are devoted to the theory of the gene, to the cytoplasmic constituents of heredity and to the evolution of the gene. Two days are devoted to discussing the production of changes in genes and chromosomes, and three days to genetic mechanisms in bacteria and bacterial viruses.

Limitations of space give a ratio of auditors to participants of 2:1. The maximum number which can be accommodated is 90 and the program lists 30 research workers from many states, from France, Italy, the British Isles, the Scandanavian countries and Yugoslavia.

EFFECTS OF WATER SOURCE ON TOXICITY OF MERCURIAL POISONS

I. Standardization of Procedure in Tests Using *Allium* Roots

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THE growing tips of *Allium* roots are now extensively utilized in toxicology and experimental cytology. This tissue was used by Macfarlane and Nadeau[8] to test antagonism of organic mercurials and potassium cyanide by cellular extracts. Thimann[13] has shown that these two types of poison inhibit plant metabolism in a similar manner. In an attempt to establish threshold concentrations for the different grades of reaction to the mercury compounds, we found that the roots were more sensitive when Cincinnati city water was used as culture medium and solvent, than in Palm Beach water. In a few tests using potassium cyanide the minimum dose which caused death, after an hour's exposure in Cincinnati was a 0.4 percent solution, while in Palm Beach 0.5 percent was required.

When the raw water supply (the affluent before purification) was used, the roots were able to resist higher concentrations of the organic mercurials than they did in the city water in both Ohio and Florida. We have investigated these phenomena further and have sought the cause of the weakened resistance to these poisons in tap water. The results are of interest in themselves, and also because of the recognized need for a standard procedure in the use of this highly sensitive, specialized growing tissue in the *Allium* test[6]. As an aid in standardization and comparison we offer a simple graded classification of the reactions of this tissue, both grossly and cytologically, to organic growth-arresting substances.

Material and Methods

Since September 1948 we have used bulbs of *Allium Cepa* L. of the selected variety Brigham Yellow Globe, grown in Colorado. Dormant bulbs were partly immersed in the water under investigation, in the dark, in jars of 200 to 300 cc. capacity. The media were renewed every second day and as soon as a good crop of roots appeared, an air space of 1 cm. was left below the base of each bulb. In small jars (50 cc.) the sensitivity increased. Variations in pH from 8.0 to 5.7 and in temperature from 20° to 28° C., in different experiments, had no noticeable effect. Examinations were made daily and an average daily increment of 1-1.5 cm. was maintained on controls for the first week after germination. Bulbs were stored in a vegetable cellar at 12°-15 C. in October and utilized until the following September. Tests were run with sets of 15 to 40 sister roots 3-10 cm. long, after removing deformed and irregular members. The poisons used were phenylmercuric hydroxide (PMOH) and basic phenylmercuric nitrate (PMN); the former was preferred because of its greater solubility. Concentrations given in continuous treatment were from 3.4×10^{-6} to 1.6×10^{-7} molar, made up from 1:3000 aqueous stock solutions, diluted always with the same water in which the roots were grown. Tests in Cincinnati were made from April to December 1949, those in Palm Beach in the first three months of 1949 and 1950. Root tips were fixed at noon or at 4 p.m., 24 hours after beginning the treatment, in 3:1 alcohol-acetic. Squash preparations were stained with propriocarmine, made permanent by dehydration in 95 percent alcohol fumes, and diaphane. Cytological analysis was made on the central region of the meristem.

Grades of Root Reaction

These organic mercurials produce terminal tubercles, or c-tumors and polyploid cells in onion root tips. These effects are similar to those of colchicine,[9, 12] but in much higher dilutions and accompanied by chromosome stickiness and some fragmentation. Three tissue regions are present in the 1 cm. root tip: Re-

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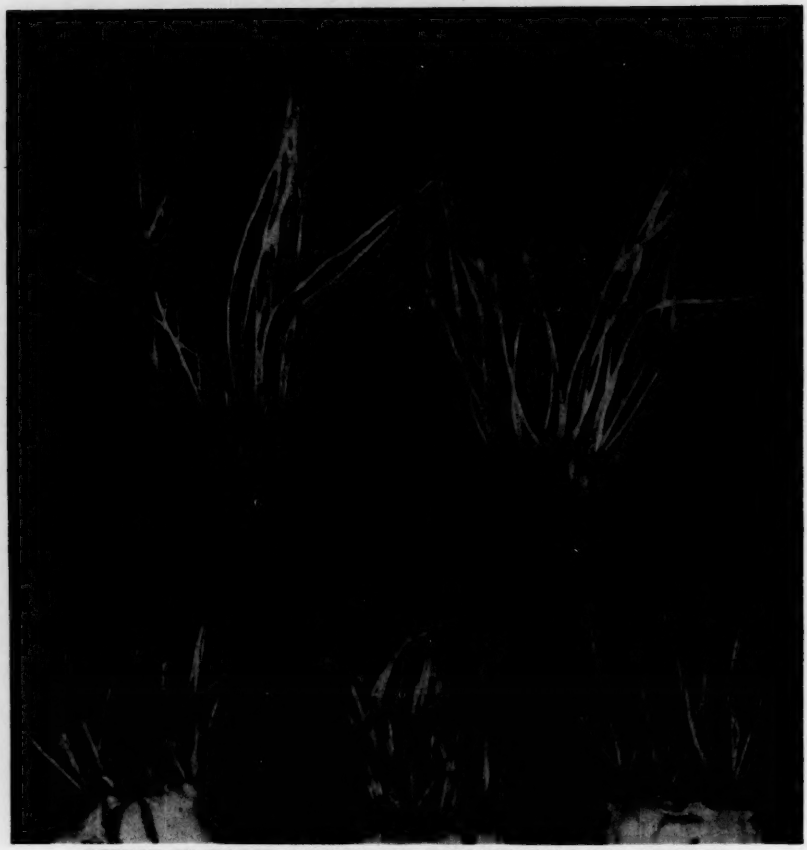

EFFECT OF WATER SOURCE AND TOXICITY ON ROOT GROWTH

Figure 20

These photographs show the difference in root development which occurred in onion roots immersed in river water and in tap water containing different concentrations of a toxic substance (phenyl-mercuric hydroxide—PMOH). When the experiment began—five days before the photographs were taken—the roots on all five bulbs were approximately 3-5 cm. long. *A* and *B* were grown in river water; *C* and *D* in tap water. *A* and *C* were immersed one hour in a 2.5 ppm (parts per million) solution of PMOH, after which growth continued in uncontaminated water from the two sources. *B* and *D* were grown continuously for five days in a 0.5 ppm solution. *E* shows development in a solution of river water containing 3-4 ppm of chlorine and 0.5 ppm of PMOH. The conditions of the roots (See Table I) are classified as follows: *A*—Grades II and III; *C*—Grade IV; *B*—Grades II and III; *D*— Grade IV, except three roots under 3 cm. in Grade III; *E*—Grades III and IV. These grades reflect macroscopic and cytological differences. Clearly the source of the water modifies the rate of growth and the condition of the treated roots.

gion 1, the lowest 1-2 mm., contains the dividing cells of the meristem; Region 2, 2-3 mm. long, contains the youngest enlarging cells which are the most sensitive to traces of poison; Region 3, the penultimate 4-5 mm., with both elongating and differentiating cells, where death first becomes apparent in lethal concentrations. Region 3 is just below the absorbing, or root hair region in soil culture, but in water culture root hairs are absent.

The gross reactions in *Grade I* are minimal. The daily growth rate is not reduced; after immersion the roots are usually slightly curved beyond a barely perceptible thickened patch. Some stimulation of growth may occur. In *Grade II* growth is arrested temporarily and a c-tumor forms in region 2. Recovery of normal growth rate is regained in two to five days (Figure 20*A* and *B*). There may be a gradual reduction in the volume of the meristem and premature production of lateral roots on some bulbs. In *Grade III* growth is arrested and the c-tumor enlarges to form a clubbed tip. There may be a slow recovery of growth, up to 50 percent of normal rate, or complete stasis (Figure 20*E*). In *Grade IV*, region 3 first becomes flaccid in one-three days, then water-logged and necrotic, with or without previous small c-tumor formation, as shown in Figure 20*C* and *D*.

The cytological reactions may also be arranged into corresponding grades.

Grade 1: some weakening of chromosome movements at late prophase and at anaphase, some stickiness and tetraploid restitution nuclei.

Grade 2: in region 2 cortical cells cuboidal and hydropic; differentiation is accelerated: in region 1; the mitotic spindle is impeded gradually the first day to give some blocked metaphases or c-mitosis and some polyploid and bi-nucleate cells. Lagging chromosomes, irregular distribution, chromatin bridges and multipolar spindles; rarely eroded or fragmented chromosomes. Polyploid restitution nuclei, micro-nuclei, poly-nucleate cells and extruded chromatin usually are present. Spindles sometimes lie diagonally indicating altered cytoplasmic viscosity. Abnormal cells are eventually outgrown by diploid cells in the later adaptation and recovery phase.

Grade 3: similar to Grade 2 in region 2; in region 1 spindle formation in all cells entering division is suppressed to give full c-mitosis. All cells may enter resting condition or mitosis may be resumed in polyploid cells. Some endomitosis in polyploid cells, which is a sign of aging[6], occurs in clubbed tips along with differentiation in short cells. Stainability of chromosomes is often reduced after mercurial treatment and nucleoli are enlarged, multiple or absent.

Grade 4: suppression of mitosis in region 1, cells already in metaphase are killed and the chromosomes run together; chromosomes in pro-metaphase fail to condense or to flex, and their heterochromatic regions are prominent.

In concentrations which are around the threshold for gross reactions of grades II to IV some roots on a bulb may be more sensitive and will enter a higher grade (Figure 20 *D* and *E*). These are usually the more rapidly growing members. Greater sensitivity with faster growth has been recorded in the colchicine literature and by Galinsky with phosphates.[2]

Resistance and Adaptation in Different Waters

The final gross reactions of roots during five days of exposure to various concentrations of PMOH in Cincinnati (C) and Palm Beach (PB) tap waters in 1949 are shown in Table I. Differential reactions in the same solution are recorded with from one to three plus signs. The greater resistance in Palm Beach water is evident; concentrations which caused only c-tumor reactions were fatal to all or some roots in Cincinnati. The minimum lethal dose in Palm Beach for Grade IV, death of all roots, was twice that required in Cincinnati. The lowest concentration to which roots could adapt with a Grade II reaction in Palm Beach was four times as strong as in Cincinnati. In some previous experiments a few roots eventually succumbed even in the lowest concentrations used in Cincinnati[9]. Concentrations of 0.1 ppm and less, in Palm Beach water, gave Grade I reaction and tended to stimulate the production of normal secondary roots on long primaries.

Similar reactions and differences in resistance were obtained when roots were exposed to solutions of PMOH 0.5 ppm to 4 ppm for an hour only and then replaced in the solvent alone (Figure 20*A* and *C*).

The reactions produced by three concentrations of PMN during five days are also given in Table I. Equimolar concentrations of the two mercurials produced approximately the same grade of reaction, but the nitrate was

TABLE I.—Gross reactions within 5 days to PMOH of roots 3-10 cm. long in tap water at Cincinnati (C) and Palm Beach (PB) in 1949, and in other solvents, (DW, glass distilled tap water; ¼ S, one quarter Shive's nutrient soln.). Treated continuously. For description of grades see text.

+ = minority. ++ = majority. +++ = 100%.

Concentration of mercurial		Solvent	Grade of Reaction I	II	III	IV
PMOH—Mole Wt						
ppm	294.6 M	C	—	+++	—	—
0.05	1.7×10^{-7}	PB	+++	—	—	—
		C		+	++	—
0.1	3.8×10^{-7}	PB or DW	++	+	—	—
		C			++	+
0.2	6.8×10^{-7}	PB		+++	—	—
		¼ S or DW		+++	—	—
		C			+	+
0.33	1.1×10^{-6}	PB			+++	—
		C				+++
0.5	1.7×10^{-6}	¼ S or DW			++	+
		PB			+++	—
		River		+	+	—
		Lake	+	+	—	—
0.8	2.6×10^{-6}	PB			+++	—
		PB				+++
1.0	3.4×10^{-6}	Lake		+	++	—
PMN—Mole Wt.						
ppm	634.44 M	C			++	—
0.1	1.6×10^{-7}	PB	+++	—	—	—
		C			+	+
0.2	3.2×10^{-7}	PB		+++	—	—
		C				+++
0.33	5.2×10^{-7}	PB		++	—	—

slightly more toxic particularly in Cincinnati. Death resulted from an hours' exposure to PMN at 5 ppm in Cincinnati and from continuous treatment in 0.33 ppm.

The greater resistance of roots to 0.5 ppm PMOH is shown in Table I, when the raw water supply in each town was used. 'River' was Ohio River water, collected at the Cincinnati Water Works in the fall; all roots survived and some recovered (Figure 20*B*). 'Lake' was water taken from Clear Lake, Florida, in which roots showed the highest resistance so far observed and survived in PMOH 1ppm. The raw waters were clear but were passed through filter paper to remove some unicellular algae.

Cytological Effects in Different City Waters

In region 1 of controls the mitotic rate was three to five percent in roots between 3 and 10 cm. long in Ohio and Florida. In Table II are shown the cytological reactions after 24 hours' exposure in Cincinnati water to nearly equimolar concentrations of PMOH and PMN. The nitrate at 0.2 ppm inhibited all spindle formation (five telophase nuclei remained among 40 mitoses) to give blocked metaphases. The hydroxide induced a stimulation of mitotic rate while impeded chromosome movements resulted in a majority of polyploid cells. These data reveal greater toxicity of the nitrate. However, the roots in PMOH were shorter than those in the PMN. A stronger polyploidogenic effect of a 0.5 ppm solution of PMOH on roots over 5 cm. long, than on shorter roots treated at the same time in Palm Beach water is demonstrated in Table II. This emphasizes the need for roots of similar length in comparing effects by the *Allium* test. Both sets of roots had reached a Grade 1 reaction cytologically in one day. The only abnormalities found, besides weakened chromosome movements, were chromatin bridges and multipolar spindles, each in only 3 percent of mitoses. Rotated spindles lying diagonally were present in both waters in three to four percent of the dividing cells in PMOH.

The roots which showed a stimulation of mitotic rate in PMOH in Cincinnati were from year old bulbs, treated in the summer of 1949 at 27° C. Ninety percent of the dividing cells contained from one to eight chromosome fragments and some extra constrictions in the chromosomes. These abnormalities resemble the structural changes and chromosome erosion produced in onion meristems by high dilutions of phenols and other compounds.[7] We found a low frequency of chromosome fragments in several experiments (e.g. Table II PMN) but multiple fragmentation was seen only in these old bulbs.

Chemical Composition and Effects

Cincinnati water is obtained from the Ohio River just above the city and Palm Beach water from surface drainage collected in Clear Lake in West Palm Beach. Both affluents are given break-point chlorination and passed through modern filtration plants where aluminum sulphate and lime are added in different amounts according to the season. The filter effluents are again chlorinated. In Cincinnati ferric sulphate is also added and the filter effluent is treated with chlorine and ammonia; there is no free chlorine in the final effluent or tap water.

PMOH at 0.5 ppm was shown to be critical for testing the effect of various media upon root resistance (Figure 20, and Table I). All roots three or more cm. long died in this concentration in Cincinnati tap water and also in the following solvents: (1) tap water passed through activated carbon filter; (2) water works filter effluent before addition of chlorine and ammonia. When the solvent was chlorinated Ohio River water (3-4 ppm Cl_2 about half of the roots died in 0.5 ppm of PMOH, but the rest survived (Figure 20*E*). Bound chlorine and chlorine gas are quickly dissipated in the water mains or upon drawing the water. A majority of the roots survived in Grade III when the solvent was glass-distilled Cincinnati tap water (DW) or quarter strength Shive's nutrient solution (¼ S in Table I), which suggests that ionic balance is involved in the differences in resistance.

Chemical analysis of the water works affluent and final effluent (tap water) for 1949 kindly supplied by the authorities at Cincinnati and West Palm Beach, are given in Table III. Passing from the best to worst with respect to root resistance, i.e. Lake, River, PB and C, there are parallel, small but progressive, increases in calcium and in chlorides, and a decrease in dissolved iron.

TABLE II.—Cytological analysis of root meristems in PMN and PMOH and tap water at Palm Beach (PB) and Cincinnati (C) after 24 hrs. exposure at 26 ± 1° C. Gross reaction Grade III.

Treatment	Total cells	Total mitoses	Mitotic rate	Per Cent: Blocked M'phase	Polypl. cells, total	Divns. with fragments	Divns. polyploid
Nil			3-5	0	0	0	0
PMN 0.2 ppm† in C(3.2×10^{-3}M)	732	40	5.5	100	11.1	2.5	70
PMOH 0.1 ppM* in C(3.8×10^{-3}M)	850	70	8.2	0	51.8	90	68.5
PMOH 0.5 ppm* in PB(1.7×10^{-6}M)	1376	42	3.1	0	0.7	0	7.1‡
Ditto †	1420	75	5.5	0	2.5	0	12.0

*Roots 3-5 cm. †Roots 5-10 cm. ‡3 prophases only

TABLE III.—Chemical analyses of water works affluent and final effluent water at Cincinnati (River and C) and at Palm Beach (Lake and PB) 1949. All values are parts per million (ppm).

	River	C	Lake	PB
Total dissolved solids	247	230	115	200.9
Total Fe	0.2	0.02	0.5	0.1
Dissolved Fe	0.1	0.0	0.8	0.14
Ca	33.9	36.4	26.6	34.8
Mg	9.5	8.5	2.6	2.2
SO_4	81.9	74.6	12.0	65.0
Chlorides	27.0	35.0	28.0	34.0
Fluoride	0.3	0.3	0.5	0.0

Discussion

All necessary nutrient elements for root growth are present in the bulb, but the aqueous medium is absorbed rapidly and the balance of ions in the latter may influence the ability of embryonic root cells to resist or adapt to traces of these poisons. The part played by mineral balance in plant nutrition is highly complex (Wadleigh[15]); but it is well established that the ratio of calcium, potassium and sodium has a direct effect upon protoplasmic permeability[3,15]. These results emphasize the importance of the aqueous medium when using onion roots as a test tissue in growth studies.

Berry[1] has substituted one quarter strength Hoagland's nutrient solution for tap water in his onion root respiration work. It might be easier for workers all over the world to use distilled water even though it slightly lowers resistance to some poisons[6].

Some authors germinate bulbs over tap water and treat in distilled water as a solvent[4,5]. We find that transfer to distilled water from tap water slows growth and is sometimes fatal to the roots, unless the change is made gradually through mixtures of the two waters. Almost any sudden physical change in the medium will impede growth. Even an hour's exposure to hypertonic solutions, namely; — twice isotonic Ringer's solution, also 0.5 percent and 1 percent yeast extract, in tap water caused Grade II gross reaction[8]. The 1 percent yeast extract produced c-mitosis with extremely short, split diplo-chromosomes as shown in some of the figures of Huskins[4] and Kodani[5]. Our colleagues have found traces of nucleic acid derivatives in this extract, however. It would seem that neither the tonicity factor, nor ionic balance in the solvent have been taken sufficiently into consideration in using the *Allium* test[4,5,10,11]. The activity of these organic mercurials in such high dilutions obviates tonicity change in the present work. The effective concentrations compare with those of the plant growth hormone naphthalene acetic acid which acts upon region *2* to arrest growth[6].

Other variables affecting the reaction of the meristem are length of root treated, rate of growth, and perhaps age of bulb. Older tissue in coleoptiles and stems was found more sensitive to these poisons by Thimann and Bonner[14]. Chromosome decay shown in fragmentation and erosion is characteristic of aging tissue in onion roots as reported by Levan and Lotfy[6]. These poisons may hasten aging of nuclei, as they obviously do cause precocious differentiatiton of embryonic root cells.

Summary

Onion roots showed a more marked loss of resistance and adaptability to two organic mercurials when Cincinnati tap water was the culture medium and solvent, than when Palm Beach water was used. In both places roots tolerated more poison in the raw water taken before purification in the water works. The imbalance of ions in the city water appears to play an important role in debilitating the tissues. The gross and cytological reactions have been described and classified into four grades. Precautions against tonicity effects and other variables are suggested in the interest of standardization of the *Allium* test.

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NEW LINKAGE GROUPS IN THE TOMATO

New Data Necessitate Revision of the Fifth, Tenth, Eleventh and Twelfth Linkage Groups.

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THE commercial importance of disease resistant varieties of the tomato has led to renewed interest in the linkage map of this plant. The mono-hybrid segregation of *Cladisporum* resistance as contrasted with the apparently multi-factorial inheritance of *Septoria* resistance make the use of chromosome markers a desirable adjunct in any tomato breeding program. In the past, one drawback to the use of these for a complete eludiation of linked genes affecting resistance has been the lack of markers in linkage groups 11 and 12. It now appears that this difficulty can be overcome since two genes have been tested with markers on the ten known linkage groups and show independent inheritance.

The tomato fruit with its wide range of size provides one of the best experimental materials for quantitative inheritance studies. Recently Fogle and Currence[3] have cast doubt on the validity of linkage group 10 by finding the gene for *wilty* in this group linked with the fifth group, *jointless*. Therefore in establishing the new linkage groups it is necessary to re-examine the data for the fifth group to see if *wilty* is or is not independent of all fifth group genes.

Plant Characters Employed

Most of the characters used in this study are fully described by MacArthur,[5] Butler[2] and Young and MacArthur.[7] Only such alterations and additions as appear necessary will be mentioned here. There are now 34 loci with known effects and linkage relations, and over 20 more are now being tested. Hence it is essential that the nomenclature should be standardized before double and triple name and gene symbols create utter chaos. The list on page seven of Young and MacArthur's monograph[7] forms a good basis for a basic nomenclature with the exception of seven symbols. In the earlier days of tomato genetics the practice arose of giving the same letter symbol to phenotypic effects rather than loci. As a consequence the following three pairs of genes now have symbols which invite confusion:

d_1—*dwarf* in linkage group 1
d_2—*dwarf* in linkage group 9
a_1—*green stem* in linkage group 5
a_2—*green stem* in linkage group 8
u_1—*uniform unripe fruit* in linkage group 7
u_2—*uniform unripe fruit* not in linkage group 7.

With increased use of the linkage map by phytopathologists and horticulturalists this symbolism may prove to be confusing, on the assumption that symbols with different subscripts refer to multiple alleles. To avoid this misinterpretation the following changes are suggested and will be adopted by the author in this and subsequent linkage papers.

A/a green stem or anthocyaninless, the former a_1 or fifth linkage group character in which the green stems are green throughout the life of the plant.

Al/al anthocyanin-loser instead of a_2 for the linkage group 8 character. The *al/al* seedlings are purple stemmed in the seedling stage but about two weeks after emerging from the soil they become green and stay green for the rest of their life.

D/d dwarf for the d_1 of linkage group 1. This is the short stocky plant habit of such varieties as Dwarf Aristocrat.

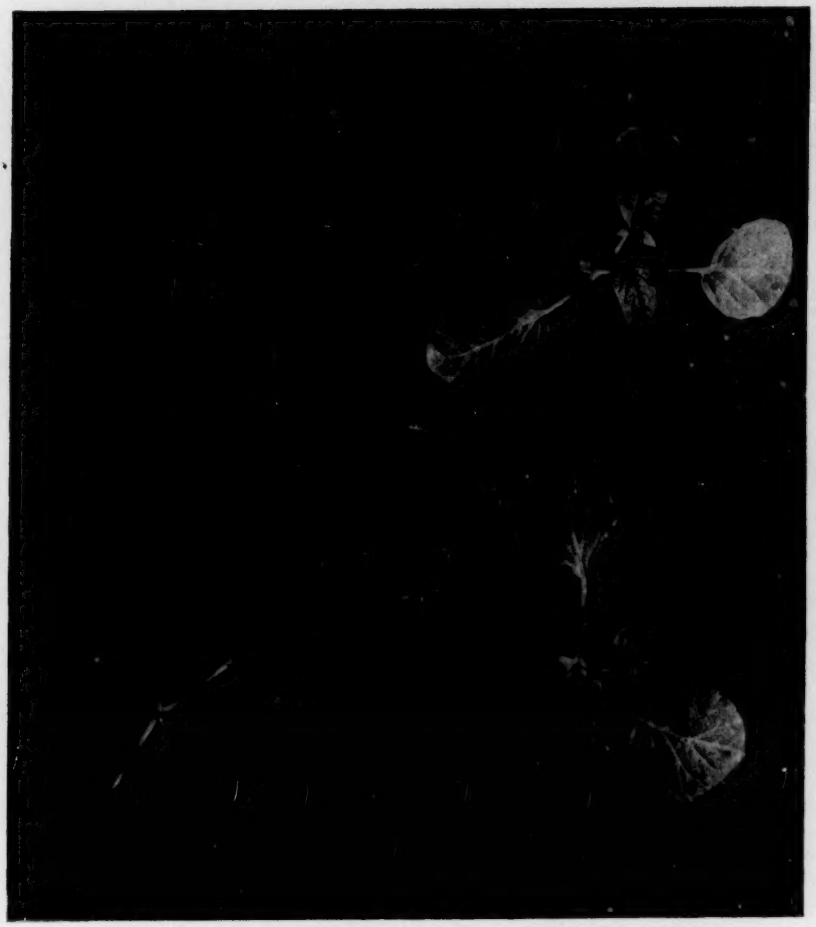
Dm/dm dwarf-modifier instead of d_2 for the linkage group 9 character found in such varieties as Burbank Preserving. This gene has no recognized phenotype in the absence of dwarf (*dd*) so is best classified as a modifier of dwarf. *DD dm dm* plants are tall, *dd Dm Dm* plants are normal dwarfs, and *dd dm dm* plants are modified or extreme dwarfs.

U/u instead of u_1 for uniform unripe fruit such as is found in the varieties Bountv and Danmark. This is in the seventh linkage group.

Ug/ug instead of u_2 for the uniform green unripe fruits found in the Uniform Globe variety. There appears to be no phenotypic difference between *u* and *ug* but Bohn and Scott[1] report that *uu* × *ug ug* gives a green-shouldered or non-uniform F_1 and a 9:7 ratio in the F_2. The linkage relations of this character are not known.

Two New Marker Genes

The two new markers reported in this paper are broaf leaf and macro-calyx. Broadleaf (*b* symbol) was obtained from Sansome under the



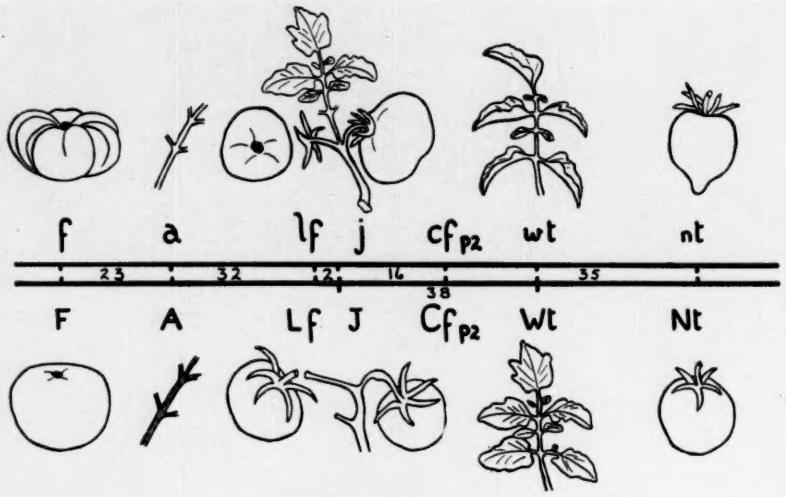
INTERACTING GENES FOR LEAF SHAPE IN TOMATO SEEDLINGS

Figure 21

Four genotypes shown here conditioned by the *C-B* gene interaction. Upper left is the *C—B—* plant; upper right is a *ccB—* plant; lower left is the *C—bb* plant and lower right is the double recessive (*ccbb*). The gene *B* has been designated as a marker for linkage group 11, and macrocalyx designated as the marker for group 12. Potato leaf is independently inherited.

name of Jorgensen's potato leaf. Sansome recognized that it was genetically different from MacArthur's potato leaf, for an F_2 involving both these markers gave a ratio of nine cut leaf to three broad leaf to four potato leaf. Careful observation makes it possible to classify the potato leaf segregates into two classes, potato leaf and broad-potato leaf with a 3:1 ratio (Figure 21). The expression of the *b* allele varies in different genetic backgrounds from a deeply cut but broader leaf to an almost entire few-lobed leaf. The first leaves are the most characteristic but the leaf types can be picked out at any stage of plant growth.

Macrocalyx (symbol *mc*) has large sepals up to six times normal size. The sepals are



LINKAGE GROUP FIVE

Figure 22

The chart shows the present location of genes in group 5. The distances given here are approximate and further data may necessitate some revision.

often inflated at the base and have broad lobes which show prominent veins. The corolla is not enlarged and appears inconspicuous in the bottom of the two inch calyx tube. The character is well illustrated in Figure 8 of Young and MacArthur.[7] In linkage studies with *mc* and the fifth linkage group characters *lf* and *j* there is trouble in classification since most macrocalyx plants also appear to have leafy inflorescences and jointless pedicels. Close inspection shows that the abscission joint is actually present but is much less pronounced than usual and often no corky layer is formed in this joint. The leafy inflorescence varies from plants which merely show a small leaf growing out of an otherwise normal flower cluster to the other extreme where the inflorescence becomes an elongated leafy stem with fruits borne singly along either side. Similar differences in expression have been noted with the allele *lf*. Both these modifications appear to be pleiotropic effects of the *mc* allele, but more work is needed before we can state which genetic backgrounds favor or suppress these expressions.

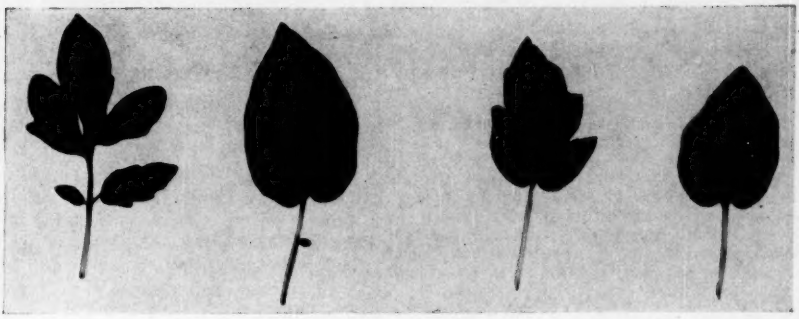
Linkage Tests

Most tests for linkage were made by crossing the new characters to three multiple recessive testers and carrying them through to the F_2. This means that most of the crosses will be in the repulsion phase. In each F_2, 400 to 1500 plants were grown and ratios of phenotypes tabulated. By means of Stevens[6] table the recombination fractions and standard errors given in Table I were calculated.*

Examination of the data in Table I show that none of the recombination fractions differ significantly from .5 so that all tests can be

*Table I containing this information is available as a supplementary document, and may be obtained by ordering Document No. 3215 from American Documentation Institute, 1719 N Street, N.W., Washington 6, D. C., remitting $1.00 for microfilm or $1.00 for 6 × 8 inch photocopies.—Ed.

The data presented in the three tables are derived from the combined results of the late J. W. MacArthur and the writer. In 1948 when Dr. MacArthur left the University of Toronto he turned over his voluminous linkage data and seed collections to the latter since he was actively engaged in the compilation of this material in the years 1933 to 1939. This mass of material has been fully analyzed and supplemented by crosses grown at the Ontario Agricultural College.



THE FOUR LEAF TYPES

Figure 23

Enlarged views of leaves showing the interactions of genes *B* and *C* shown in Figure 21. The order is as follows: *B—C—*, *B—cc* genes, *bbC—* and *ccbb*. The potato leaf gene tends to produce a compound leaf in the presence of *C*. Secondary leaflets are produced in plants carrying allele *B*.

assumed to show no linkage. This permits the use of these two genes as markers of the two remaining linkage groups in the tomato. Broadleaf is designated as the marker for linkage group 11 and macrocalyx the marker for linkage group 12.

It should be emphasized however that further data may force a revision of these designations. These results do not preclude the possibility that broadleaf and macrocalyx are at the opposite ends of the chromosomes from any of the marker genes used in linkage groups 2, 4, 6, 8, 9, or 10. It is hoped that by the end of another season enough additional data will have been accumulated to establish firmly the framework of the twelve linkage groups of the tomato.

The fifth and tenth linkage groups contain the following characters:

Group 5		*Group 10*	
Fasciated fruit	*f*	Wilty foliage	*wt*
Green stem	*a*	Nipple tip fruit	*nt*
Leafy inflorescence	*lf*		
Jointless pedicel	*j*		
Cladosporium resistance	Cf_{p2}		

The recombination data are given in Table II and show that *f a lf j* are definitely linked with each type of cross giving substantially the same crossover value. In no case are the recombination values from the three types of crosses as much as two standard errors apart. Further evidence for the linear order of these loci is given in Table III. Here the recombinants from two back-crosses are tabulated. It will be seen from this table that the linear order *f a lf* gives the minimum number of double cross-overs there being 39 as compared to 61 double cross-overs given by the other possible order *a f lf*. The recombination fraction for *f lf* is significantly smaller than expected from the Kosambi formula. For F_2 coupling the value from the formula is .429 as opposed to the actual of .390 $\pm$ .013.

The jointless locus is a little harder to place. It is definitely close to *lf* as shown by the F_2 coupling segregation of *L fJ* 3753:*Lf j* 32: *lf J* 90: *lf j* 1236. The corresponding chi-squares for mono-hybrid segregation are 2.43 for the *lf* locus and 0.099 for the *j* locus. Both are a good fit, the discrepancy in *lf* being due to an excess of the recessive leafy inflorescence. This character is variable in its expression so that the inequality in the recombinant classes of 32 : 90 is probably the result of *jj Lf lf* genotypes being sometime classified

TABLE II. Recombination fractions for linkage group 5.

Type of Cross		Genes *a*	*lf*	*j*	*wt*
F_2 coupling	*f*	.230±.023	.394±.009	.390±.013	.463±.011
repulsion		.296±.022	.368±.051	.404±.066	
B.C. coupling		.221±.022	.321±.042		.527±.042
F_2 coupling	*a*		.329±.016	.324±.016	
repulsion			.370±.028	.345±.055	.524±.029
F_2 coupling	*lf*			.027±.022	.405±.009
					.537±.042
F_2 coupling	*j*				.376±.012

TABLE III. Backcross recombinants for the linkage group 5 loci *F, A,* and *Lf*.

F_1 Genotype	Recombinations *None*	*Region 1*	*Region 2*	*Region 1 & 2*	*Total*
$\frac{F\ A\ Lf}{f\ a\ lf}$	163	39	65	12	279
$\frac{F\ a\ Lf}{f\ A\ lf}$	167	61	96	27	351
Total	330	100	161	39	630

$$F\ A\ \frac{139}{630} = .2206 \qquad A\ Lf\ \frac{200}{630} = .3174$$

as *lf*. MacArthur[5] places *j* on the same side of *lf* as the *a* locus while Langford[4] places it on the opposite side. Most of these data favor MacArthur's view but the critical back-cross data are not available.

The recombination data for *wt* is not as clear-cut. Positive linkage is shown in F_2 data between *wt* and *f*, *lf*, and *j*. The back-cross data show no such linkage but since they consisted of only 134 plants and the notes show difficulty in the classification of the *wt* segregates, it can be set aside. The F_2 data are based on 2,607 plants in the case of *wt j* and 5,835 plants for *wt lf*. The data and chi-squares for the two F_2's are:

J Wt 1583 : 367 : 416 : 241		*Lf Wt* 3521 : 939 : 900 : 475	
χ^2 *J/j*	0.056	χ^2 *Lf/lf*	6.41
χ^2 *Wt/wt*	3.916	χ^2 *Wt/wt*	1.83
χ^2 linkage	83.89	χ^2 linkage	98.91

This shows that although there is a major discrepancy in the *lf* monohybrid ratio caused by a deficiency in the *Wt lf* class, and a minor deficiency in the *wt* segregates, by far the largest portion of the partitioned chi-square is in the linkage component. There is also a significant linkage between *f* and *wt*. The F_2 repulsion cross of 630 plants shows no linkage between *a* and *wt* although the error is large enough that loose linkage of 47 percent could be expected. These data would indicate that *wt* is on the opposite side of *lf* from the *a* locus. This means that linkage group 10 is no longer valid. It is interesting to note that the four recessive mutants *f lf j* and *wt* all occur in the variety Rouge Naine Hative which is listed in eighteenth century seed catalogues.

The data for the other tenth chromosome character, *nipple tip*, are rather meager. With *wt* they show an F_2 segregation of *Nt we* 374 : 94 : 66 : 50 which gives a shortage of *nt* segregates and a cross-over value of 35 per cent. With *green stem* the *nt* recombination fraction is .496 ± .031. With *lf* the only data available are some notes of MacArthur giving a segregation of 167 :72 :61 :19 with no information as to whether they are coupling or repulsion data. If coupling they give a cross-over value of 54.6 percent and if repulsion a cross-over value of 45.3 percent. This would indicate that probably *nt* is on the far side of *wt* which would make this chromosome about 150 units long. While the exact placing of these loci will have to await the outcome of a six point back-cross presently being prepared, the linear order and approximate distances are as given in Figure 22.

New Linkage Alignments

In view of these data, MacArthur's linkage group 10 is no longer tenable: it should be combined with linkage group 5. The markers broad leaf and macrocalyx are not assigned to the tenth group to replace wilty, as they were in use for two years as markers of group 11 and 12 before it was suspected that group 10 was not a bona fide group. It is expected that a mutant "narrow cotyledon (*nc*)" will become the new marker for the tenth group. It appears independent of all known groups but more data are needed to rule out the possibility of loose linkage in two cases.

Summary

Two characters which show no linkage with the known groups are now placed as markers in linkage groups 11 and 12. The character broad leaf is placed in 11 and macrocalyx in 12.

Wilty in the tenth group is shown to be linked with characters in the fifth linkage group so these two groups should be combined. The recombination values indicate that *wt* is on the opposite side of *lf* from the *a* locus and that *nt* is probably on the distal side of *wt*. New symbols are suggested to overcome the confusion caused by the symbols a_1 and a_2, d_1 and d_2, u_1 and u_2.

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A METHOD FOR ANALYZING MULTIPLE ALLELIC INHERITANCE

In Dizygotic Twins

D. C. RIFE*

DIZYGOTIC twins provide the geneticist with two types of valuable information. First, they are used extensively in comparisons with monozygotic twins as a means of estimating the heritability of various traits. Secondly, they may be used to check simple modes of inheritance, although they have not been utilized extensively for this purpose. Dizygotic twins may be placed in three categories in respect to a trait: pairs which are concordant for the possession of the trait, pairs which are concordant for its absence, and discordant pairs. The ratio of these classes of dizygotic twins depends upon the mode of inheritance of the trait, and upon the frequencies of the genes in the general population. Formulae have been derived and tables are available which show the proportions of the three types of dizygotic twins at various gene frequencies for simple dominance, lack of dominance, sex linked, and sex influenced inheritance (Rife[2]). The purpose of this paper is to show how data from dizygotic twins may be used in a similar manner to check multiple allelic inheritance, where there is graded dominance.

There are two matings which can result in discordant pairs, where simple dominance is concerned. These are $Aa \times Aa$, *and* $Aa \times aa$. Let p = frequency of gene A, and l-p the frequency of gene a. Then the frequency of mating type $Aa \times Aa = 4p^2(1\text{-}p)^2$. Among pairs of dizygotic twins from such matings, 6/16 or $1\frac{1}{2}p^2(1\text{-}p)^2$ should be discordant. The frequency of mating type $Aa \times aa = 4p(1\text{-}p)^3$. Half of the dizygotic pairs of twins arising from these matings may be expected to be discordant. Thus the expected proportions of dizygotic pairs of twins $= 1\frac{1}{2}p^2(1\text{-}p)^2 + 2p(1\text{-}p)^3$.

Suppose we have three alleles, A, a', and a, with dominance decreasing in the order listed. As A is dominant to both a' and a, we may employ the formula $1\frac{1}{2}p^2(1\text{-}p)^2 + 2p(1\text{-}p)^3$, to estimate the sum of the proportions of twins discordant for A— versus a'—, plus those discordant for A— versus aa. This leaves the discordant pairs resulting from matings of $a'a \times a'a$ and $a'a \times aa$ to be accounted for. Letting p = frequency of A, q = frequency of a', and r = frequency of a, the proportion of twins discordant for a'— versus aa may be easily estimated. The matings, their frequencies, and the frequencies of discordant pairs are shown below:

Mating	Frequency	Frequency of discordant pairs of offspring, a'– versus a– only
$Aa \times a'a$	$8pqr^2$	pqr^2
$a'a \times a'a$	$4q^2r^2$	$1\frac{1}{2}q^2r^2$
$a'a \times aa$	$4qr^3$	$2qr^3$

Total frequency of discordant pairs of offspring from above matings is:

$$a'a \text{ versus } aa \text{ only}, = pqr^2 + 1\tfrac{1}{2}q^2r^2 + 2qr^3$$
$$= qr^2(p + 1\tfrac{1}{2}q + 2r), \text{ then since } p = 1 - (q + r),$$
$$= qr^2(1 + \tfrac{1}{2}q + r).$$

The total proportion of discordant pairs will then equal $1\frac{1}{2}p^2(1\text{-}p)^2 + 2p(1\text{-}p)^3 + qr^2(1 + \frac{1}{2}q + r)$. Table I shows the expected proportions of discordance among dizygotic twins at various gene frequencies, where three

TABLE I. The proportions of discordance among dizygotic twins for traits due to three multiple alleles with graded dominance, at various gene frequencies. Frequency of p = 1 — (q + r).

Frequency of q	r = .10	.20	.30	.40	.50	.60	.70	.80	.90
.90	*.01395*								
.80	.16995	*.05120*							
.70	.19242	.20135	*.10395*						
.60	.28035	.27920	.25245	*.16320*					
.50	.26595	.30095	.31295	.29395	*.21875*				
.40	.22395	.28160	.32595	.34560	.32795	*.25920*			
.30	.16695	.23495	.29835	.34365	.36695	.32935	*.27195*		
.20	.10635	.17360	.24395	.30720	.35195	.36560	.33435	*.24320*	
.10	.05235	.10875	.17535	.24195	.29795	.33135	.32895	.27815	*.15795*

Frequency of r

*The Ohio State University, Institute of Genetics.

multiple alleles with dominance are concerned. The figures in italics on the diagonal show the percentages of discordance where only two alleles are involved. Here $p = 0$, and $q + r = 1$. The highest discordance shown is .27195, where $q = .3$ and $r = .7$. Values for p for all combinations not represented by underlined $q + r$ values can be obtained by application of the formula $p + q + r = 1$. The highest discordance shown for three alleles is .36695, where $p = .2$, $p = .3$, and $r = .5$.

It can be shown that the amount of discordance depends upon the number of alleles in the series and their frequencies. The greater the number of alleles in the series, the greater will be the maximum proportion of discordance. The amount of discordance will seldom exceed 50 percent, however, regardless of the number of alleles in the series.

Matings of type $Aa \times a'a$, in which both parents are heterozygous, but for different dominants, are the only ones which may be expected to result in more than 50 percent discordance. Although the discordance is 62½ percent from such matings, only a portion of matings within any population may be expected to be of this type. If significantly more than 50 percent of a series of pairs of dizygotic twins show discordance in respect to an inherited trait, it may be assumed that the variation is not due solely to a simple series of multiple alleles with a graded order of dominance.

While the value of twins as a tool to measure heritability is well known and widely used, the light which dizygotic twins shed on modes of inheritance is frequently overlooked. For example, Kiil[1] investigated the inheritance of direction of frontal hair. He conducted a thorough study of several families and came to the conclusion that the three phenotypes are conditioned by a series of three multiple alleles. His family data gave strong support to this hypothesis. He also compared 30 pairs of monozygotic and 28 pairs of dizygotic twins. Complete concordance was observed in the monozygotic twins, but the dizygotic twins manifested 57 percent discordance. Kiil correctly interpreted these data as evidence that the direction of frontal hair is due solely to heredity. But he apparently overlooked the dizygotic twin data, in which 16 pairs out of 28 were discordant, to be a means of confirming or disproving the triple allelic mode of inheritance.

The three allelic genes postulated by Kiil showed approximate freqeuncies of $p = .14$, $q = .20$, $r = .66$. We should expect approximately 36 percent of pairs of dizygotic twins to show discordance in such a population. This would mean that approximately 10 rather than 16 pairs of the 28 should have shown discordance. The deviation from the expected is quite significant, having a Chi-square value of 5.6. This observation strongly suggests that two or more sets of alleles are responsible for the direction of frontal hair.

Summary

1. If variation in a trait is due solely to a single pair of alleles with dominance, dizygotic twins should not manifest more than 28 percent discordance.

2. If variation in a trait is due solely to a series of three multiple alleles, dizygotic twins should not manifest more than 38 percent discordance.

3. If dizygotic twins manifest more than 50 percent discordance in respect to a genetic trait, it is more than likely that genes at two or more different loci are involved.

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Department of Utter Metaphorical Confusion

Soviet Science Division

"BUT the steam-roller of the Lysenko 'revolution' did not stop there. . . . Having torn their robes in sadness that they were not, after all, such good Marxists as they had thought, and having sprinkled ashes thick on their weary crania, the editors tried to blow up a few straws to clutch."—Joseph Brozek, *Science*, April 14, 1950, p. 391.

MONOPLOIDY IN NICOTIANA

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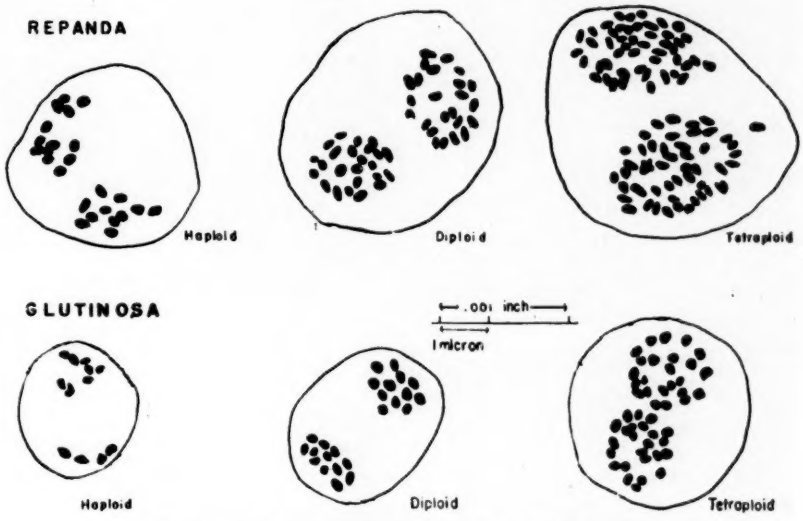


NUCLEI OF *REPANDA* AND *GLUTINOSA* 'PLOIDS
Figure 24

Here are shown pollen mother cells of the haploid, diploid and tetraploid plants of the two *Nicotiana* species described in the text.

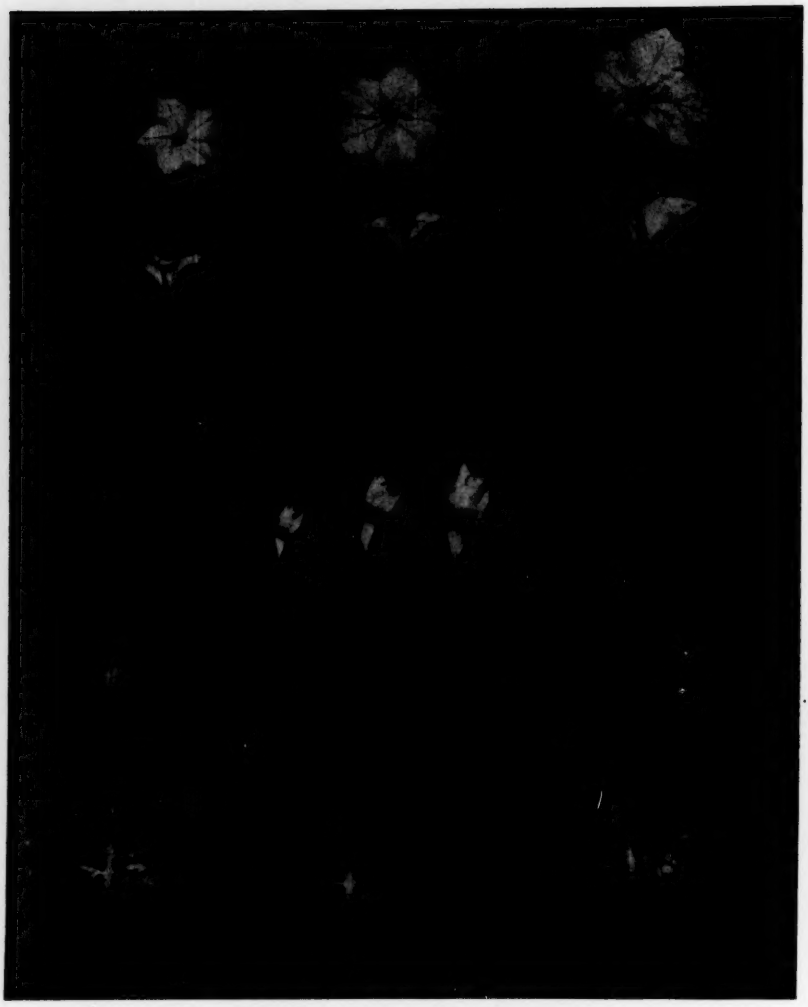
SINCE the first monoploid plant was found in *Datura* in 1922,[2] similar plants with only one set of chromosomes have been described in at least fifty-six species of flowering plants. A list of these plants by families and genera is shown in Table I.

Monoploidy is used here to denote the 1*N* condition that exists when the nucleus is composed of a single set of chromosomes representing only one complete genome of a single species. As thus defined[5] the term is not necessarily synonymous to the condition that exists when an individual develops with the gametic number of chromosomes. This latter condition—designated by the term haploidy, with a 1*X* chromosome number—can occur in either polyploid plants where more than one basic genome is involved, or in diploid plants. Monoploidy, on the other hand, is largely restricted to diploid plants.

Induction and Origin

Monoploidy or haploidy have been successfully induced most frequently by using X-rayed pollen or pollen from another species or genus. Pollen from a plant with another ploidy has likewise

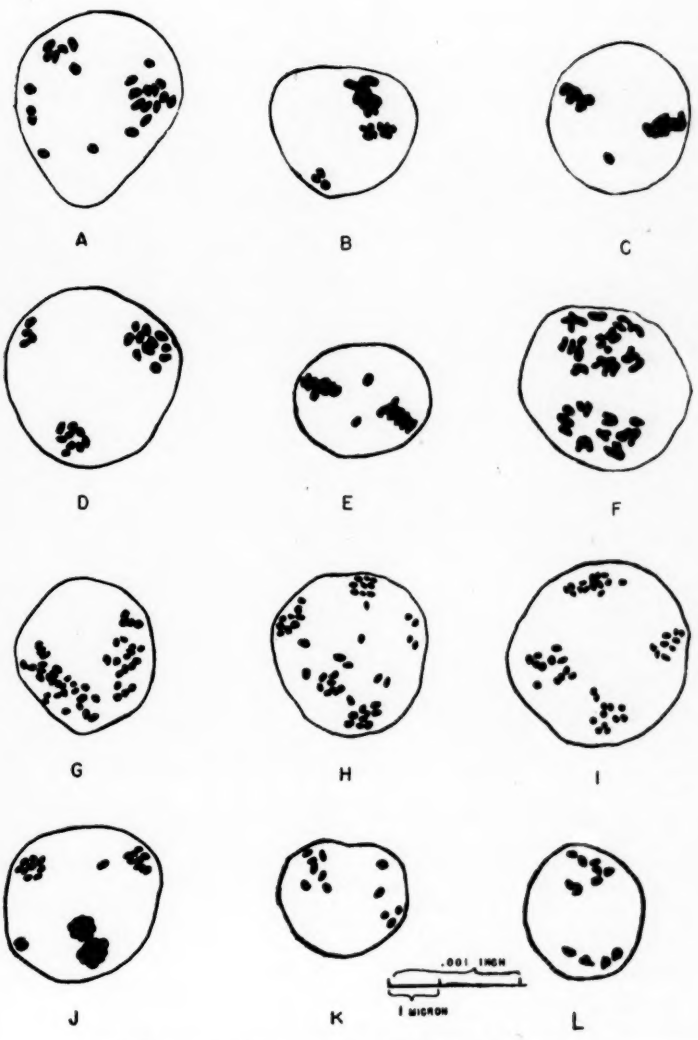
*Published as Paper No. 262, Department of Plant Breeding, Cornell University, Ithaca, New York. The author wishes to acknowledge the assistance of Dr. H. H. Smith, Cornell University in preparing this manuscript for publication and for his advice and encouragement.



'PLOIDY IN *NICOTIANA* SPECIES

Figure 25

A shows haploid, diploid, and tetraploid flowers of *Nicotiana repanda*. *B* shows flowers and leaves of the same series of *N. glutinosa*. The monoploid plants of *N. repanda* and *N. glutinosa* were obtained among four viable seedlings from a cross between an *N. repanda* male and an *N. glutinosa* female. The *repanda* monoploid has *repanda* chromosomes and *glutinosa* cytoplasm. The haploid plants are shown in Figure 27.



MEIOTIC DIVISION IN THE MONOPLOID PLANTS

Figure 26

These drawings show meiotic division in the two monoploid plants shown in Figure 27. *A-J* show nuclei in *N. repanda*. *K-L* show meiosis in the *glutinosa* monoploids.

often been reported to initiate the development of a haploid plant. Less successful methods include heat or cold treatments at the time fertilization occurs, the use of colchicine, and delayed pollination after emasculation.

From a cytological point of view haploidy results from aberrations in the normal reproductive process. In the fifty-six species (Table I) haploidy arose as follows (some species appear in two classifications):

Development of reduced female cells without syngamy, or loss of a complete set of chromosomes after syngamy	49
Polyembryony	15
Development of the male gamete without syngamy	3

Nicotiana Monoploids

The monoploid condition has been reported in five species of *Nicotiana: N. tabacum, N. rustica, N. glutinosa, N. langsdorffii,* and *N. sylvestris.* There is ample evidence that the two species, *N. tabacum* and *N. rustica* are of remote natural amphidiploid ancestry and that plants of these two species developing with the gametic number would not be true monoploids since the nucleus would contain more than one set of chromosomes of a single species. There is no question that the plants described by Kostoff[3] which have the gametic number of chromosomes from the amphidiploids, *N. rustica-paniculata, N. glauca-langsdorffii,* and *N. sylvestris-tomentosiformis,* were not true monoploids since they were composed of two genomes from two different and known parental species, and as such, were essentially F_1 interspecific hybrids.

An Unusual Case of Monoploidy

In the spring of 1949 the cross *N. glutinosa* (♀) and *N. repanda* (♂) was made in the greenhouse. The cross, not previously reported, produced very few seeds, most of which were inviable. These seeds were treated (along with all other supposedly F_1 seeds) with a 0.4 percent aqueous solution of colchicine for twenty-four hours at the time the radicle was emerging from the seed coat. A total of four plants was obtained:

4989–1 F_1 interspecific hybrid with intermediate flower characters.
4989–2 Normal diploid *N. repanda.*
4989–3 Monoploid *N. glutinosa* (Figures 25 and 27).
4989–4 Monoploid *N. repanda* (Figures 25 and 27).

Field notes on these plants gave the following data:

Plant 4989-1 (F_1 *N. repanda* × *N. glutinosa*)
Stem: rudimentary, plant about three inches high, making only a rosette of sessile leaves.
Flowers: only two produced, light pink in color, intermediate between the two parents having a longer tube than *N. repanda* but retaining zygomorphic pink flower of *N. glutinosa,* (These flowers were not measured and none have since been produced.)
Plant: very slow growing, dwarf in growth, sterile.

Plant 4989-2 (Diploid *N. repanda*)
Stem: Woody, much branched, approximately 28 inches in height.
Leaves: Sessile, distributed along the stem.
Flowers: White with inside of throat a deep reddish purple, flowers closed during the middle of the day, 28 mm across corolla, tube 45-50 mm in length, flowers nearly regular, slightly lobed, tube long and thin.
Plant: Vigorous, self fertile and setting large amounts of viable seed. Similar in all respects to normal plants of *N. repanda.*

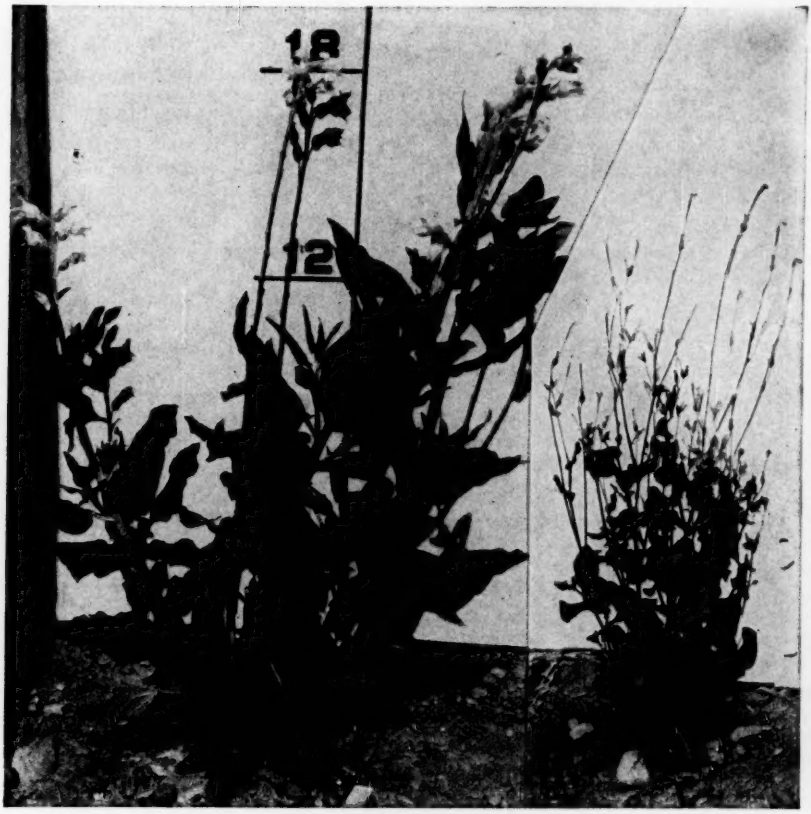
Plant 4989-3 (Monoploid *N. glutinosa*—Figure 27)
Stem: Semi herbaceous, branched, 19 inches in height.
Leaves: Petiolate, subcordate and somewhat pointed at the apex, distributed along the stem, slightly pubescent.
Flowers: Light Pink (lighter than the diploids), highly zygomorphic, 18 mm in length.
Plant: Vigorous, blooms profusely, completely self-sterile with pollen almost 100 percent aborted. Similar to diploid *N. glutinosa* but more dwarfed in all parts.

Plant 4989-4 (Monoploid *N. repanda*—Figure 27)
Stem: Woody, much branched, 16 inches in height.
Leaves: Sessile, distributed along the stem.
Flowers: White with inside of throat a deep reddish purple, flowers closing during the middle of the day, corolla 16 mm across, tube 24-28 mm in length, corolla somewhat more pointed than in diploids, tube long and thin.
Plant: Fairly vigorous, self sterile and pollen nearly 100 percent aborted. Similar to diploid *N. repanda* but more dwarfed in all parts. Short vegetative life.

TABLE I. Angiospermous Plants in Which Haploidy has been Described.

Family	Genus*
Chenopodiaceae	Beta (1)
Compositae	Crepis (2)
Convolvulaceae	Pharbitis (1)
Cruciferae	Brassica (1), Matthiola (1)
Fumariaceae	Fumaria (1)
Gramineae	Aegilops (1), Dactylis (1), Hordeum (2), Oryza (1), Phleum (1), Poa (1), Secale (1), Stipa (1), Sorghum (1), Triticum (8), Zea (1).
Liliaceae	Asparagus (1)
Linaceae	Linum (1)
Malvaceae	Gossypium (3)
Nolanaceae	Nolana (1)
Onograceae	Epilobium (1), Godetia (2), Oenothera (6)
Portulacaceae	Portulaca (1)
Rubiaceae	Coffea (1)
Scrophulariaceae	Antirrhinum (1), Digitalis (1)
Solanaceae	Capsicum (1), Datura (1), Lycopersicum (1), Nicotiana (5), Solanum (3)

*The number of species in which haploidy has been described is given in the parentheses.



MONOPLOID PLANTS

Figure 27

On the left is shown a monoploid plant of *N. glutinosa* (4989-3). On the right is shown a monoploid plant of *N. repanda* (4989-4). Of the four seedlings which grew from a cross between these two species one was a hybrid, one was a normal diploid *repanda* which must have arisen by male androgenesis, and two were the plants shown above.

Cytology of the Plants

Cytological examinations of meiosis were made of the three plants 4989-2, 4989-3 and 4989-4. The salient findings are as follows:

Plant 4989-2 (Diploid *N. repanda* in *N. glutinosa* cytoplasm.)

Meiosis was found to be nearly normal. At diakinesis there were 24II followed by 24I at each pole of anaphase I. The only abnormality noted was some laggards at the anaphases in about 20 percent of the cells. However, the pollen was good indicating that normal cells were formed. No effect of *Nicotiana glutinosa* cytoplasm could be detected in the plant. This plant could have arisen either by the androgenetic development of an unreduced male gamete or by doubling of an androgenetic monoploid. In view of the colchicine treatment of the seeds the latter explanation seems more likely.

Plant 4989-3 (Monoploid *N. glutinosa*)

This plant exhibited irregularities at meiosis similar to those completely described by Webber.[7] Briefly these were:

Diakinesis: 12I formed.

Metaphase I: 12I form a weak metaphase plate.

Anaphase I: Reduction division at random ranging from 12 <> 0 to 6 <> 6. In Figure 26*L* is shown 5 <> 7 and in Figure 26*K* is shown 4 <> 8.

Metaphase II: Univalents split and move toward opposite poles.

Anaphase II: Equal distribution of univalents, no laggards. Those cells with 12I form viable pollen.

Plant 4989-4 (Monoploid *N. repanda*—*Figure* 27)

This plant was in many respects similar in its meiotic behavior to the *glutinosa* haploid. It was not so vigorous, however, and died soon after being brought into the greenhouse. For this reason it was possible to study fewer stages of meiosis.

Metaphase I: Many cells exhibited 1-3 laggards which usually were left at the metaphase plate, and in later divisions were not incorporated in the daughter nuclei.

Anaphase I: Reduction division was at random and the 24I were distributed to two or more poles. In Figure 26*D* there are shown cells with a univalent distribution of 4, 9 and 11 to three poles, and a distribution of the 24I to two poles is shown in Figure 26*B*, *C*, and *E*. The division in Figure 26*A* exhibits the lack of orderly bipolar distribution that is characteristic of many cell divisions during meiosis. Laggards are shown in cells C, E, and J. In the latter cell the splitting of one laggard is visible.

Metaphase II: The univalents split without forming a definite metaphase plate as seen in Figure 26*F* and *G*. Typical cells at Metaphase II are shown in Figure 26*E* showing laggards from the first division.

Anaphase II: Univalents move to opposite poles in a random manner in some cells, resulting in unequal distribution to sister nuclei as in Figure 26*I*. The lack of regularity in the second meiotic division is shown in Figure 26*H*.

Origin of the Monoploids

The *N. glutinosa* monoploid could have arisen either by reduced parthenogenesis or by gynogenesis[5] since it exhibited only the characteristics of the maternal parent in reduced size.

The monoploid *N. repanda* could have arisen only by the development of the male nucleus in the egg sac of the female parent. It is, therefore, definitely an example of androgenesis.[5] The fact that both reduced parthenogenesis (or gynogenesis) and androgenesis occurred in the same cross might lead one to postulate the possibility of the male nucleus entering the egg but with syngamy failing, and both the male and female gametes developing independently in the same egg sac.

Loss of chromosomes, including the appearance of haploids, following colchicine treatment has been previously reported.[1,4,6] It is possible that the monoploid found here could have been induced by the action of colchicine, though it is difficult to see how an entire genome of one species would be lost, leaving the genome of the other species intact.

Another *N. glutinosa* monoploid was found in a population of 51 F_1 plants of the cross *N. glutinosa* (♀) × *N. sylvestris* (♂). This monoploid was identical both phenotypically and cytologically to the one already described, and probably arose through parthenogenesis, though the seed was colchicine-treated, and this treatment may have again been a possible cause of monoploidy.

Attempts to Repeat the Cross

In the summer of 1949 a total of 50 crosses were made using *N. glutinosa* as female and *N. repanda* as male as in the original cross. A scanty supply of seed was harvested. Furthermore, in the winter of 1950, ten crosses were made in the greenhouse, but all the plants from these latter crosses died in the seedling stage.

Ploidy and Plant Vigor

As can be noted in Figure 25, with an increase in the number of duplicated chromosomes, there is a corresponding direct increase in general size of flowers, leaves, and pollen mother cells. Furthermore, in general the vigor of the plants increased in the same manner although the 4*N N. repanda* was somewhat slower growing than the 2*N N. repanda*. The monoploids were both sterile, and produced no selfed seed. The diploids in both cases set more seed than the tetraploids; the 4*N N. glutinosa* was highly infertile.

Summary

From the cross *N. glutinosa* (♀) × *N. repanda* (♂), a total of four plants were obtained as follows: a true F_1 interspecific hybrid, a diploid *N. repanda*, a monoploid *N. repanda*, and a monoploid *N. glutinosa*. The diploid *N. repanda* is believed to have arisen either as the result of colchicine doubling of an androgenetic monoploid, or by the functioning of an androgenetic unreduced male gamete. This plant arose from a *N. repanda* nucleus in *N. glutinosa* cytoplasm. The monoploid *N. repanda* must have developed by androgenesis, while the monoploid *N. glutinosa* was the result of either gynogenesis or parthenogenesis. Meiosis in the two monoploids was extremely abnormal, while the diploid *N. repanda* had almost normal meiosis. The haploids were sterile and lacked vigor.

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